

THE EVOLUTION OF ANTIPREDATOR BEHAVIOR IN
SNAKES: ULTIMATE AND PROXIMATE
DETERMINANTS

By

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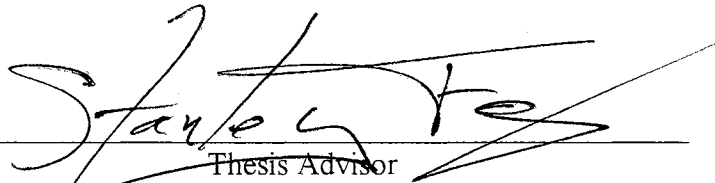
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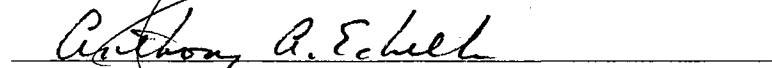
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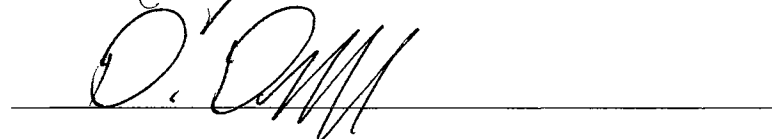
Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
May, 2002

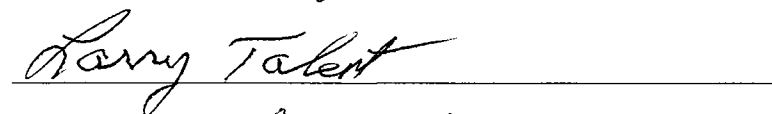
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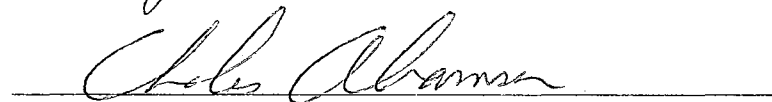
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ACKNOWLEDGMENTS

I would like to thank my major advisor, Dr. Stanley Fox, and committee members, Dr. Anthony Echelle, Dr. David Duvall, Dr. Larry Talent, and Dr. Charles Abramson. I am indebted to Montgomery Bruner, Daren Riedle, Joy Yoshioka, David Underwood, Melissa Stangland, Kenneth Cole, Edward Hara, Lenn Shipman, and Ron Shipman for assistance in the field and help with scoring the many hours of videotaped snake behavior. This work was carried out with the support of an Oklahoma State Regents for Higher Education dissertation improvement grant and a doctoral scholarship from the Southern Region Education Board. I thank my parents, Ron and Connie Shipman, for their moral support and encouragement. Most of all, I thank my wife Lori for being by my side and for her patience and support, and my children, Alexandra and Alan for the joy that they bring me and for helping to remind me of the really important things in life. Last, I thank God, the first and last ultimate determinant, for providing me wonderful puzzles.

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THE EVOLUTION OF ANTIPREDATOR BEHAVIOR IN PITVIPERS:
ULTIMATE AND PROXIMATE DETERMINANTS

Despite their being limbless, snakes exhibit the most diverse antipredator behavior found among reptiles (Shine et al, 2000; Greene, 1994a). This, ironically, may well be a result of the necessity for creative solutions (adaptations) to avoid predation in lieu of the more standard modes of predator escape afforded by limbs.

Most published information on antipredator tactics in snakes is based on single-species studies with the relatively abundant natricine colubrids, most notably, gartersnakes (Shine et al., 2000). Few publications deal exclusively with the study of antipredator behavior in pitvipers (but see Graves and Duvall, 1988; Goode and Duvall, 1989), even though several species occur in sufficiently high densities to make them attractive among snakes as subjects for research.

Descriptions of antipredator behavior in snakes, particularly tail displays (Greene, 1973, 1994a), are well documented. Specialized and stereotyped antipredator behavior in snakes includes death feigning, envenomation, cloacal popping, cloacal sac discharge (musk), coiled tail displays, S-coil defensive postures, body balling and other

tightly coiled defensive postures, tail vibration, mouth hissing, and dermal sound production (Greene, 1994a).

Although herpetologists have long known that snakes often exhibit highly repeatable, stereotypic antipredator behavior, there has been no comparative study based on directly measured observations of such behavior. Greene (1979, 1994b) and Jackson et al. (1976) suggested broad generalized trends in the predictability of antipredator behavior in snakes, but they did not explicitly address the effects of phylogeny. Greene (1979) reported that fossorial and terrestrial snake taxa that were not necessarily closely related converged toward one pattern of tail and head displays, and arboreal and semi-arboreal snake taxa converged toward a different pattern. Greene (1994b) also compared open-mouth threat displays of viperids in a more updated phylogenetic context. Jackson et al. (1976) used multivariate techniques to identify behavioral-ecological variables that maximally discriminated between morphological groups of snakes based upon dorsal pigmentation patterns. While comparative in nature, data were qualitative scorings of morphological and behavioral-ecological variables for all species of snakes north of Mexico and were taken from personal field observations and the literature. Behavioral variables were

more important than habitat in distinguishing among dorsal pigmentation patterns.

Other studies of antipredator behavior in snakes have dealt with with descriptions and, to a limited extent, factors correlating with antipredator behavior (Greene, 1973; Arnold and Bennett, 1984; Sweet, 1985; Golani and Kochva, 1988; Brodie, 1989; Herzog et al., 1989; Herzog and Schwartz, 1990; Schieffelin and de Queiroz, 1991; Brodie, 1992; Savage and Slowinski, 1992). All of these previous studies of antipredator behavior in snakes used very simple and easily observed behavior such as the number of open-mouth strikes, escape speed, escape direction, latency to strike, and latency to escape.

Factors shown to affect or correlate with antipredator behavior in snakes are habitat (Greene, 1979; Golani and Kochva, 1988; Duvall et al., 1985); morphology and color patterns (Greene, 1973; Jackson et al., 1976; Brodie, 1992); geographic variation (Sweet, 1985; Herzog and Schwartz, 1990); ability of the snakes to see the eyes of a potential predator (Herzog and Bern, 1992; Greene, 1994a; Burger, 1998); movement and size of threat stimuli (Scudder and Chiszar, 1977; Herzog et al., 1989); incubation temperature (Burger, 1998); body temperature (Arnold and Bennett, 1984; Goode and Duvall, 1989; Schieffelin and De

Queiroz, 1991); reproductive status (Graves, 1989); social context (Duvall et al., 1985; Graves and Duvall, 1988); interspecific differences (Brodie, 1989; Herzog et al., 1989); and phylogeny (Greene, 1979, 1994b).

The intercorrelation of ultimate (historical and evolutionary) and proximate (developmental and environmental) causes has confounded attempts to understand relationships between these factors and antipredator tactics of snakes. This is owing to the fact that causation in biological systems occurs simultaneously at different levels (Duvall and Beaupre, 1998).

Questions concerning the origin of biological diversity in physiological, morphological, and behavioral phenotypes are commonly framed at two conceptual levels, ultimate and proximate (Mayr, 1993). Ultimate questions ask *why* a group of organisms exhibit a particular trait or character and proximate questions are aimed at *how* those traits or characters are expressed during the lifetime of an individual (Alcock, 1993). This current characterization of ultimate and proximate questions subsumes Tinbergen's (1963) four epistemological categories of causation (proximate), ontogeny (proximate), survival value (ultimate), and evolution (ultimate). In a logical fashion, the agents invoked to address these questions are

referred to as ultimate and proximate causes. Ultimate causes include more distant evolutionary history (phylogeny) and the adaptive significance that led to the evolution of particular traits, and proximate causes are the more immediate causes and developmental controls of the expression of those traits.

Ultimate causes include factors such as evolutionary history (phylogeny), life history mode, sex, and morphological characters such as adult body size, color pattern, and anatomical structures (i.e., presence or absence of a rattle). These are factors that *have brought about* or coevolved with adaptive behavior through past action of evolution and this behavior is now displayed by contemporary individuals that inherit these factors. Proximate causes include factors such as microhabitat, ontogeny, previous experience with predators, social context, reproductive stage, body temperature, and body condition (health, presence or absence of a food bolus, stage of ecdysis, etc.). These are factors that *bring about* specific behavior, or elicit it, in contemporary individuals experiencing one state or another of these influences that change during an individual's lifetime.

A conceptual framework for addressing these problems using an integrative approach has existed since the time of

Aristotle, was employed by Darwin, and reiterated more recently (1970 to present) by others (Duvall and Beaupre, 1998). However, this integrative approach is seldom put into practice because of the perceived difficulty and historical constraints of computational power. Recent technological advances and the development of new statistical approaches (Fox and Shipman, in press) has put this ideal approach within the grasp of researchers willing to accept a paradigm shift in the way that research is conducted (Duvall and Beaupre, 1998).

Specifically addressing the problems encountered in the study of snake antipredator behavior, a way to deal with the intercorrelation of ultimate and proximate factors would be to simultaneously measure these factors and attempt to partition out the relative amount of variation attributable to the separate effects. In the context of a comparative study, this approach would support broad, general inferences about the evolution of antipredator behavior in snakes and the ultimate and proximate factors that influence it.

In such an approach, relationships among multiple ultimate and proximate factors and antipredator behavior are assumed to exist a priori. In other words, it is assumed that to some as yet unknown amount, factors such as

phylogeny, sex, body size, body temperature, and body condition are related to specific types of antipredator behavior. The questions asked are not then primarily focused on asking *if* these relationships exist, but *why*, *how*, and *to what extent* these factors are related.

Addressing these questions requires 1) some knowledge of the phylogenetic relationships of the taxa being considered (derived from independent data), 2) observations of other ultimate factors and control and/or measurements of proximate factors, and 3) a method to quantify the antipredator behavior in a common currency.

Part of the frustration with conducting research on the antipredator behavior in snakes is due to the difficulty in collecting enough empirical data. This a problem inherent to snake studies due to the arduous task of obtaining suitable numbers of observations on often sparse and secretive populations of snakes, leading to a phenomenon referred to as "lizard envy" (Siegel, 1993). I agree with Siegel (1993), who acknowledges these difficulties, but additionally argues that "lizard envy" results from "1) not recognizing the limitations of snakes for certain kinds of studies, 2) not using different and innovative techniques when it is apparent that traditional techniques are inadequate, 3) not properly matching

question, study animal, and technique, and 4) not focusing on the aspects of snake biology that make them 'model' organisms for certain kinds of research."

Despite these limitations, snakes are, in various ways, ideal for studies of factors affecting antipredator behavior. Many aspects of snake behavior and morphology are no doubt primarily driven by the selective forces of predation, or the relative lack thereof, as hinted by the well-documented, diverse, and highly specialized antipredator behavior found among snakes. This applies also to venomous snakes. Despite the potential cost to predators, venomous snakes are also subject to predation and predation is a driving selective force in their behavior and morphology since many predators have evolved traits to counter the risk of envenomation (Greene, 1992).

Perhaps one of the most notable derived antipredator adaptations in snakes is the rattle, an epidermal, sound-producing structure found on the tip of the tail in 29 species of rattlesnakes. Defensive behavior in the repertoire of a basic viper includes crypsis, locomotor escape, striking, biting, and envenomation (Greene, 1992). Other derived antipredator characters found in vipers include the stereotypical S-coil found in rattlesnakes, and open-mouth threats (Greene, 1992).

The derived venom delivery systems of elapids and viperids most likely evolved first as an adaptation to aid in the capture, handling, and digestion of prey (Greene, 1992, 1994a; Kardong, 1996). However, there has also been coevolution between the use of venom for defense and other stereotyped antipredator behavior, i.e., tail rattling and open-mouth threats. Pitvipers, subfamily Crotalinae, family Viperidae, share a set of distinct heat-sensitive facial pits and derived characters with other members of Viperidae, indicating that this taxon has not evolved within a colubrid lineage (Campbell and Brodie, 1992). Primarily for these reasons, pitvipers as a group deserve separate treatment in a comparative study.

In this paper, I present an integrative comparative study of antipredator behavior on 10 species of pitvipers in four genera. My objectives were to 1) quantify the antipredator behavior of snakes of different species by exposing them to a standard, graded, threat stimulus, 2) determine the evolution and phylogenetic components of antipredator behavior, and 3) remove the effects of phylogeny and test relationships between ultimate and proximate causative factors and antipredator behavior.

METHODS

Capture of snakes

My goal was to quantify antipredator behavior in as many individuals and taxa as time and resources would permit. I made experimental observations of antipredator behavior on 177 pitvipers of ten species across four genera. I employed several techniques of capture with standard post-capture handling at three general geographic locations: southeastern Arizona, west-central Arkansas, and southern Mexico.

I made three separate 10-day field excursions to southeastern Arizona to collect data for this study (August and September, 1995, and August, 1996). I captured snakes primarily by road cruising between 1900 and 2400 hrs on a 25-km section of Highway 80, 45 miles north of the city of Douglas in Cochise County. This locality has been an excellent area to obtain snakes for study by other workers (Mendelson & Jennings 1992). The work at this locality yielded observations on a total of 85 pitvipers of five species (Table 1).

From 1996 to 1997, I conducted trials on snakes captured during another unrelated research project. Snakes were collected during diurnal, visual plot surveys in the Ouachita Mountains, north of Hot Springs, Arkansas, in

Garland and Perry Counties five times a year from May 1995 to March 1999: early May, late May, mid-June, early October, and early the following March. I made experimental observations on 85 snakes of four species during this work (Table 1).

Snakes were captured at various locations in the states of Veracruz and Yucatan, Mexico, during November, 1996, mostly by road-cruising. My effort in this area yielded the fewest number of snake captures and observations, resulting in only six observations on one species.

Snakes were picked up with the aid of plastic snake tubes, or in some cases, with snake tongs, and then placed individually into clean cloth sacks. These sacks were laid into 30-gallon coolers with damp paper towels to prevent dehydration and then transported to a convenient outdoor site where trials were conducted and body measurements were taken. While awaiting processing, the snakes were kept in their individual sacks in the shade in open coolers or on the substrate.

Experimental techniques

I recorded the proportion of time (in seconds) that individual snakes spent in specific postures or actions while exposed to a standardized threat stimulus. Usually

within 24 hours, but never longer than five days after their capture, I allowed snakes to acclimate to ambient temperature before placing them individually into a shaded, portable 1-m x 1-m neutral arena in the field. I then used a standard threat stimulus (Scudder & Chiszar 1977; Herzog et al. 1989; Bowers et al. 1993) to begin the trials.

My standard threat stimulus was a set of snake tongs fitted with an effigy of a generalized canine predator head constructed of foam rubber, covered with lycra material, and equipped with hobby eye-buttons. The mouth was outlined with canid-style teeth constructed from dense foam rubber. My choice of predator stimulus was made to provide a controlled, standardized threat with which to assay behavior, thus precluding the use of live predators. It has been shown in previous studies with snakes and lizards that the exact shape of a predator stimulus is largely insignificant; rather, the movements and elevation of the stimulus are most important (Bustard, 1979; Herzog et al., 1989; Shine et al., 2000). Harry Greene has achieved repeatable results by subjecting snakes to the threat of a rubber Bart Simpson doll fitted onto the end of snake tongs (personal communication). Several researchers have used the human hand as a predator stimulus (Shine et al., 2000)

but this technique was not considered due to the concern for safety with the venomous taxa being studied here.

Snakes were exposed only one time each to a 3.5-minute trial with the following sequence of escalating levels of threat: no threat, no visible predator or observer, duration = 30 seconds; potential threat, observer moves to the arena and visually orients to snake, duration = 30 seconds; pre-capture threat exposure, predator lowered into the arena and situated one body length (of the snake in the arena) away from the snake - lateral to the snake if snake not coiled and facing snake's head if snake coiled, duration = 30 seconds; predator threaten, predator model thrust toward the snake (but not touching) at a rate of one thrust per second, duration = 30 seconds; pre-capture predator touch, snake touched with predator model mid-body at a rate of one touch per second, duration = 30 seconds; predator grasp, snake gently picked up and lifted 50 cm (half the distance to the top of the arena) into the air and then placed back down, duration = single event usually lasting three to five seconds; post-capture predator touch, as pre-capture predator touch, duration = the remainder of a 30-second period beginning at predator grasp, usually 27 - 25 seconds; post-capture predator exposed, predator model movement stopped, duration = 30 seconds. The timing of

each threat stage was made with a multiple-alarm laboratory timer. I personally conducted all trials. Resulting behavior was recorded with a Canon ES800 8-mm video camera that I held while conducting each trial. Video data collection began at the potential threat stage.

Snakes were removed from the arena at the termination of each trial. I recorded several parameters for each snake after each trial: body temperature (immediately recorded after the trial using a quick-reading cloacal thermometer), snout-vent length (measured by stretching snake along measuring tape), sex (determined by probing), stage of ecdysis (post-molt, inter-molt, or pre-molt determined by visual inspection), presence or absence of a food bolus (determined by palpation), presence or absence of evidence of previous injury (visual inspection), and reproductive status of females (palpation). Ventral scales of all snakes were clipped for future identification should they be recaptured to prevent running multiple trials on any individual. Snakes were then returned unharmed to their site of capture and released.

The video data yielded a total of 8.8 hours of footage. I evaluated and scored the behavior of each snake from video tape in detail (frame by frame). Video tapes were viewed using a Sony EV-A50 8-mm video recorder and a

19-inch television monitor. I initially used an open-ended catalogue to record body postures, antipredator displays, and actions (Table 2), noting the position of the snake's head, anterior body (from head to center of mass), posterior body (from center of mass to vent), and tail during a trial (Arnold & Bennett 1984). Head, body, and tail positions were scored relative to their relative positions and orientations to the predator and to each other. I scored behavior beginning at the predator-exposed threat level and ending upon termination of the post-capture predator-touch threat level. Behavior at distinct stages of the trial were not separately analyzed. This resulted in two minutes of scored behavior for each snake. A posture, display, or action was scored as the number of seconds it occurred in the two-minute period. After all video data were collected, I transformed these values into the proportion of time a snake exhibited these postures, displays, and actions during a trial. Extremely rare behavior was omitted prior to data analysis. Behavior was defined as rare if it was exhibited by fewer than three individual snakes (regardless of species) out of all 177 snakes, or if it occurred less than an average of 1% of the time in all trials.

Phylogenetic Hypothesis

My ability to identify the phylogenetic components of antipredator behavior hinged upon reference to a "good" phylogenetic hypothesis. Among snakes, the phylogenetic relationships among pitvipers - particularly rattlesnakes - have been well studied, although no published phylogeny currently exists that includes all ten species of my study. However, all of these species have been studied in various phylogenetic contexts and several monophyletic groups using biogeographical, morphological, and molecular data are well supported (Gloyd, 1940; Brattstrom, 1964; Klauber, 1972a; Foote and MacMahon, 1977; Stille, 1987; Knight et al., 1993; Parkinson, 1999; Parkinson et al., 2000; Bushar et al., 2001, Murphy, et al., in press). I constructed an hypothetical phylogeny with equal branch lengths by assigning my species to their monophyletic groups and then placing those groups according to the best supported relationships with each other (Figure 1). The result was a conservative phylogenetic hypothesis. Snake membership in these monophyletic groups was coded as dummy variables for use as covariables in CCA II to remove the effects of common ancestry (phylogeny) in the variation of antipredator behavior. The covariable categories were: *Bothrops*, *Agkistrodon*, *Sistrurus*, and *Crotalus*.

Analytical methodology

Over the past few years, many researchers have returned to the idea that comparisons of species as independent evolutionary units invite Type I statistical errors. Consequently, several methods are being developed to statistically address comparative questions by referencing to or controlling for the constraints of phylogeny (see reviews in Huey, 1987; Pagel and Harvey, 1988; Gittleman, 1989; Burghardt and Gittleman, 1990; Funk and Brooks, 1990; Gittleman and Kot, 1990; Brooks and McLennan, 1991; Harvey and Purvis, 1991; Miles and Dunham, 1992; Losos and Miles, 1994; Martins and Hansen, 1997).

Miles and Dunham (1992: 848) stated "Because life history traits are likely to be correlated with a species' phylogenetic history, unequivocal evidence for adaptation to local environmental conditions may be recognized only after the variation in a trait attributable to phylogeny is removed." This applies as well to antipredator behavior in snakes. Thus, in order to deduce the ultimate and proximate factors that influence antipredator behavior in snakes, observations must be viewed alternately both within and outside of the constraints of phylogeny.

I used canonical correspondence analysis (CCA) to gauge the phylogenetic components of antipredator behavior

in pitvipers and test for relationships with ultimate and proximate factors after subtracting the variation due to phylogeny. Use of CCA in this context has recently been advanced (Fox and Shipman, in press).

Canonical correspondence analysis is a direct-gradient ordination technique commonly used in community ecology (ter Braak 1988; Palmer 1993; ter Braak and Šmilauer, 1998). It is used to study the occurrence of species found at sampled sites responding in order to environmental gradients that are input as independent continuous or categorical variables. The scores from CCA can be plotted to infer how sites with similar species composition relate to the measured environmental variables and can be easily interpreted graphically by overlaying the scores of sites (plotted as points), species (plotted as points), and environmental variables (plotted as vectors). Sites with similar species composition are grouped together and placed in order along the environmental gradients that best explain or correlate with the observed patterns. Essentially, CCA can be thought of as a special case of multiple regression.

In using CCA for studying antipredator behavior in pitvipers, I redefined the variables: individual snakes are "sites" or sample plots, postures, displays, and

actions are "species" or dependent variables, and the ultimate and proximate factors are the "environmental" or independent variables. In such an analysis, individual snakes with similar postures, displays, and actions will be ordinated relative to the ultimate and proximate independent variables.

I conducted two primary CCA tests. The first (CCA I) was designed to identify phylogenetic patterns of antipredator behavior and compare these patterns to the relative influences of other ultimate factors (species-specific body size, sex, and presence or absence of a rattle). The influences of proximate factors (body temperature, reproductive condition, evidence of injury, and presence of a food bolus) on antipredator behavior were removed in this CCA by using them as covariables. This partial ordination factors out the amount of variation in the observed antipredator behavior that is due to the estimated influence of these proximate factors, leaving the rest of the variation to be explained by the ultimate factors. Partial ordination is analogous to a partial correlation in multiple regression. To identify phylogenetic patterns, behavior patterns best associated with each species in the CCA were mapped onto a phylogeny (see Phylogenetic Hypothesis above) and Farris character

optimization was employed to estimate ancestral and derived behavioral traits (Brooks and McLennan, 1991).

The second CCA (CCA II) removed the variation in antipredator behavior attributable to phylogeny and was used to examine the relative importance of the remaining ultimate factors plus the proximate factors in explaining antipredator behavior. Partial correlation is an accepted phylogenetic-subtraction method (Pagel and Harvey, 1988). Here, phylogenetic subtraction was accomplished by using membership in monophyletic clades identified a priori as categorical variables and then using them as covariables in partial ordination. This factored out the variation in antipredator behavior resulting from the pattern of common ancestry, leaving the rest of the variation to be explained by the remaining factors. With the exception of the species category variable, the other ultimate factors were retained in this analysis since their influences on antipredator behavior are to some unknown degree correlated with phylogenetic history. In other words, the relationships of these ultimate factors with particular antipredator behavior may be obscured by the overriding influence of phylogenetic effects and might not be apparent unless those phylogenetic effects are first removed. For example, body size (snout-vent length), now becomes a

proximate factor as the ontogenetic stage of growth, since the inter-generic differences in adult body size are factored out as a covariable.

To perform these analyses, I used the statistical software package CANOCO 4.0 for Windows (ter Braak and Smilauer, 1998). CANOCO 4.0 performs Monte Carlo permutation tests to evaluate the significance of relationships between dependent and the independent variables at two levels. The first tests the overall significance of the relationship between the dependent variables and the sum of all canonical axes, with the null hypothesis being no significant relationship between antipredator behavior (dependent variables) and independent variables combined. The second tests whether each ordination axis based on independent variables shows a significant relationship with the dependent variables. In my case, the null hypothesis was no relationship between antipredator behavior and the CCA axis under consideration. Because I conducted two separate CCAs, one to identify phylogenetic components and relative influence of ultimate factors, and the other to compare effects of proximate and ultimate factors (after removing effects of phylogeny) on antipredator behavior, I employed the Bonferoni adjusted p-

value (0.05/2) as the critical value to reject the null hypothesis for either test.

RESULTS

Phylogenetic relationships of antipredator behavior

For CCA I, there were significant relationships among behavior patterns and the sum of all axes (Monte Carlo test with 9999 permutations, $F = 4.10$, $p = 0.0003$) and there were significant relationships between individual axes 1-4 and the observed patterns of behavior (Table 3).

The scores of snakes on the first four axes of CCA I demonstrated highly species-specific patterns of antipredator behavior, with overall intra-specific variation being less than inter-specific variation (Figures 2-4). The scores also indicated that antipredator behavior in the three small-bodied species of rattlesnakes, *C. pricei*, *S. miliarius*, and *S. catenatus*, was more similar to that of non-rattlesnake species than to that of the four large-bodied species of rattlesnakes.

Axis one explained the greatest amount of variation in behavior, with axes two, three, and four explaining sequentially less variation as indicated by their eigenvalues, which are a measure of the relative strength

and importance of an ordination axis and the amount of variation explained by the axis (Table 3). The overall relationships between the independent variables and specific patterns of behavior are found by examining the position of the plotted behavior patterns with respect to the independent variables. Behavior patterns that are plotted far beyond the independent-variable vectors and isolated from the other behavior patterns represent relatively rare behavior and should not be used for inference of overall trends, but may be informative for describing apomorphic behavior for individual species. Behavior patterns located close to the origin of the axes are ubiquitous and also less informative for describing overall patterns. Therefore, the interpretation of the overall pattern is taken from the types of behavior that are most closely associated with the termini of the vectors of independent variables.

As ultimate independent variables, the presence or absence of a rattle, and, collectively, the species-category variables explain the greatest amount of variation in antipredator behavior (Figure 5). Behind these, snout-vent length appears as an ambiguous factor, since small and large species are associated with each other along any given axis. The ultimate variables for sex (male or

female) had very short vectors, indicating their minimal importance, and so were not plotted in this first analysis.

The first axis (Table 4, Figure 5) showed that behavior diverged primarily on the basis of the presence or absence of a rattle and membership to one of the four large-bodied taxa of *Crotalus* vs all other taxa. On axis one, snakes with high negative scores (far left) were large-bodied *Crotalus* species that exhibited more elevated tails that were positioned more centered on their bodies, elevated anterior bodies, more protected or hidden heads positioned more centered on their bodies and facing the predator, loosely coiled body postures, and escaped directionally away from the predator more. Snakes with high positive scores (Table 4, Figure 5, far right) were both *Agkistrodon* species and *Sistrurus catenatus*, which had more depressed tails positioned more distal to the predator, more depressed anterior bodies, more exposed heads positioned more lateral to and oriented away from the predator, more open body postures, and escaped directionally toward the predator. *S. miliarius*, *C. pricei*, and *Bothrops asper* were intermediate in these behavior patterns along axis one.

Along axis two (Figure 5), variation in behavior was determined primarily by species differences between *S.*

miliarius, *B. asper*, and *Agkistrodon piscivorous* vs *A. contortrix*. Snakes with negative scores, *A. contortrix* (bottom), had more straight posterior body postures, positioned their heads proximal to and oriented more lateral to the predator model, and presented more open-mouth strikes. Snakes with high positive scores along axis two, *S. miliarius*, *B. asper*, and *A. piscivorous* (top), exhibited tail wriggling behavior (especially *A. piscivorous*) and more tightly coiled bodies (Table 4).

Axis three (Figure 6) distinguished the behavioral differences of *S. miliarius* and *B. asper* vs *A. piscivorous*. With high positive scores on axis three, *S. miliarius* and *B. asper* exhibited more asymmetrical body coils and had more instances of tails hidden from view. *A. piscivorous*, with high negative scores, displayed mouth gaping more and escaped more laterally from the predator (Table 4).

Axis four (Figure 7) maximally expanded the behavioral differences between *C. pricei* and *B. asper*. *C. pricei* had derived tail displays of curling their tails and exposing the ventral surface of the tail to the predator. They also positioned their heads more distal to the predator, and positioned their tails more proximal to the predator (Table 4).

I was able to map major modes of antipredator behavior for head orientation, head position, anterior body elevation, overall body posture, tail elevation, tail exposure, tail position, and escape direction onto the phylogeny (Figures 8-15). I was not able to map several behavioral characters because they were either too ubiquitous across all species or were too apomorphic to be phylogenetically informative. The most ubiquitous and hence, plesiomorphic characters, were tail vibration, posterior body depressed, open-mouth strike, tail positioned lateral to predator, tail exposed, head depressed, head elevated, and body stationary. Apomorphic characters were the derived mouth-gaping behavior of *A. piscivorous* and the specialized tail coil and ventral tail exposure of *C. pricei*. Tail rubbing behavior occurred in four species (*C. horridus*, *C. atrox*, *C. scutulatus*, and *S. catenatus*), but did not seem to fit explanation by any of the axes, other than seeming to be more associated with the large-bodied rattlesnakes.

Proximate and ultimate causes of antipredator behavior

The second CCA tested for the relationships of ultimate and proximate factors with expressed antipredator behavior after removing the effects of phylogeny. Overall relationships of all axes with behavior were significant

(Monte Carlo test with 9999 permutations, $F = 1.64$, $p = 0.001$).

The relationship of behavior patterns specifically with axes one and two were significant (Table 5). After removing the effects of phylogeny, the presence or absence of a rattle disappeared as a significant determinant of antipredator behavior. Also, the presence or absence of a food bolus did not significantly explain variation in antipredator behavior.

On axis one (Table 6, Figure 16), behavior patterns ranged from generally more active with elevated tail displays (left) to more passive (right). Gravid snakes performed more tail rubbing behavior, had more depressed tails more proximal to the predator, more depressed and exposed heads, escaped less directionally toward or away from the predator, vibrated their tails less, and exhibited open-mouth strikes less than non-gravid snakes. Warmer snakes had more open body postures, escaped more lateral to the predator, had more exposed and depressed heads, more depressed tails, and vibrated their tails less than cooler snakes. Snakes with evidence of previous injury had more coiled body postures, heads positioned more centered on their bodies or distal to the predator, coiled tails more centered on their bodies or proximal to the predator, and

exhibited less open-mouth strikes than snakes without evidence of previous injury.

Along axis two (Table 6, Figure 16), behavior modes ranged from more open body postures and active defense (top) to more protected body postures with aposematic displays. Males, larger snakes, snakes in intermolt stage of ecdysis, and snakes with evidence of previous injury (high negative scores) exhibited more tail and mouth displays, with tails and heads positioned more centered on the body, more instances of head hide, more elevated anterior bodies, more coiled body postures, and delivered open-mouth strikes less often than females, smaller snakes, and snakes without evidence of previous injury. Females, smaller snakes, and snakes in the postmolt stage of ecdysis had more open body postures, delivered more open-mouth strikes, positioned their tails more distal to the predator, hid their tails more often, and positioned their heads more proximal to the predator.

Sex and stage of ecdysis were highly correlated with snout-vent length in their association with antipredator behavior. Correspondingly, in all but three species in this study, adult males were larger than adult females and sex correlated with snout-vent length. Stage of ecdysis may be correlated with body size because smaller snakes

with faster growth rates shed more often than large, adult snakes. Thus, the chance of finding smaller post-molt snakes is greater than finding adult post-molt snakes. This may have implications for the effects of evidence of previous injury on antipredator behavior along axis two as well. The chance of finding evidence of a previous injury is greater in larger, older snakes, resulting in a correlation between evidence of injury and snout-vent length.

To test if these correlated factors had any explanatory power by themselves, I conducted a third CCA by repeating CCA II with snout-vent length as an additional covariable instead of an independent variable. While the overall relationship of all axes remained significant (Monte Carlo test with 9999 permutations, $F = 1.51$, $p = 0.001$) and the observed patterns along axis one remained the same (Monte Carlo test with 9999 permutations, $F = 4.66$, $p = 0.0007$), sex (male or female) and molt stage factors disappeared as explanatory variables and axis two was not significant (Monte Carlo test with 9999 permutations, $F = 2.35$, $p = 0.267$). No additional explanation of variance along axis two was attributed to sex or molt stage once variation due to body size was controlled for. The relationship of evidence of previous

injury with antipredator behavior as a factor by itself was significant in its explanatory value only along axis one. Its effect in explaining variation along axis two, like sex and molt stage, appears to reflect its correlation with snout-vent length; larger/older snakes would have more accumulated evidence of previous injury than smaller/younger ones.

DISCUSSION

The observed species-specific response of snakes underscores the importance of incorporating phylogeny into a study of antipredator behavior of these pitvipers and confirms the utility of my methods to interpret patterns among species. Prior to any discussion, however, it is important to review the constraints and framework of my study design.

Responses of snakes to the predator effigy were predictable and repeatable, but they may differ from responses to a real predator in the natural environment. Although the behavior seemed directed toward the predator effigy, I was in partial view of snakes during all trials and may have affected their responses. Still, it would not be feasible to conduct a comparative study with real predators in an experimental setting, and it is unlikely

that enough observations of encounters between snakes and their actual predators could be observed, let alone quantified, in field studies since such observations are extremely rare (Jackson et al., 1976). Moreover, researchers of antipredator behavior in snakes generally concur that repeatable responses are observed regardless of the physical make-up of predator models used (Shine et al., 2000). Future studies might experimentally manipulate cues presented by predator models. Habitat context, a factor shown to influence antipredator behavior in snakes (Greene, 1979; Golani and Kochva, 1988; Duvall et al., 1985), was artificial (but controlled) in this study. Habitat structure in the arena could also be manipulated in future studies. Lastly, all of these snakes rely first on crypsis and the avoidance of detection by predators as an antipredator strategy. In my study, I focused on the post-detection antipredator behavioral repertoires of pitvipers. Previously, such studies have only examined simple measures of incidence of biting or escape behavior. Even with these constraints and limitations, however, my data supplied patterns such that broad and general inferences could be made about the evolution of antipredator behavior in pitvipers and the ultimate and proximate determinants associated with that behavior.

Evolution of antipredator behavior in pitvipers

By mapping species-specific behavior patterns onto a phylogeny, I was able to use character optimization to estimate the ancestral states for several antipredator responses in pitvipers. These ancestral states are as follows: head facing more away from predator (Figure 8), head positioned more centered on body (Figure 9), anterior body more depressed onto the substrate (Figure 10), body more coiled (Figure 11), tail less elevated (Figure 12), tail more centered on body (Figure 14), and escape direction more toward a predator (Figure 15).

Many of the behavioral modes also contained synapomorphic states and therefore are potentially useful for making phylogenetic inferences. As such, they should be added to morphological, molecular, and other behavioral data for the development of a more complete and robust phylogenetic hypothesis for these species. Behavioral modes that contained synapomorphies were head orientation (Figure 8), anterior body elevation (Figure 10), tail elevation (Figure 12), tail position (Figure 14), and escape direction (Figure 15). Four of these synapomorphies occurred with the immediate ancestor of the four species of large-bodied rattlesnakes. These included head facing more towards the predator (Figure 8), anterior body more

elevated (Figure 10), tail more elevated (Figure 12), and escape directionally away from predator (Figure 15). Any trained herpetologist (and many laypersons) would recognize these as components of the well-described, stereotypical, elevated S-coil and backward crawl found in rattlesnakes. The peculiar aspect of this observation is not that these snakes exhibit this behavior, but that the three small species of rattlesnakes do not exhibit it and in fact are more similar to the non-rattlesnakes in their antipredator behavior than to the large-bodied members of the rattlesnake clade.

It is generally assumed that the evolution of the rattle constituted a major and unique divergence in antipredator tactics in snakes (Greene, 1992). As such, I expected that the rattle would be associated with a suite of behavioral responses unique to all rattlesnakes. My assessment indicates, however, that the specialized behavior associated with the use of the rattle coevolved with increased body size within the rattlesnake clade.

Determining the selective forces and incipient function that led to the evolution of the rattle has received recent attention (Schuett, 1984; Fenton and Licht, 1990; Cook et al., 1994, Young and Brown, 1995; Sisk and Jackson, 1997). Three general hypotheses about the

evolution of the rattle have been described. The earliest and most currently accepted hypothesis is that the rattle evolved as an aposematic signal to warn potential predators and large, grazing ungulates that might step on the otherwise unnoticed snake of its venomousness and potential danger (Hay, 1887; Klauber, 1972; Greene, 1992). A more recent suggestion (Schuett, 1984) is that the incipient rattle evolved as an improvement for the caudal luring of prey, a behavior exhibited by many pitvipers and a few colubrids (Greene, 1994a). Sisk and Jackson examined these hypotheses by evaluating sound production and attractiveness to prey of the supposed bi-lobed tail tip precursor to the rattle and the more common conical tail tip of pitvipers, but they were unable to find support for either a difference in sound or attractiveness to prey. The third and less popular hypothesis is that the rattle evolved as an enhancement to a caudal display to distract aggressors away from the head (Garman, 1890; Williams, 1966). I use commonly held concepts of behavioral ecology, previous literature, and my own data to argue against the former two hypotheses and lend support to this latter idea.

It is easiest to dismiss the caudal lure hypothesis as an incipient function of the earliest rattle (Greene, 1994a). There is currently no evidence to suggest that a

rattle or proto-rattle functions as an enhancement to caudal luring (Sisk and Jackson, 1997). In fact, there is indirect evidence contrary to this in that adult rattlesnakes seldom, if ever, engage in caudal luring (Greene, 1994a). If the rattle evolved first as an enhancement to caudal luring, I would expect there to be some evidence of at least a residual function in this capacity.

An aposematic signal is a form of communication, or advertisement, to a predator or other aggressor that there is a net cost for interference with the signaler. In this way, the predator learns to associate the aposematic cue with a painful experience and will in the future avoid animals that exhibit that signal. Or, in the case of a lethal cost to the transgressor, a species may evolve an innate avoidance to the aposematic signal. To fit the criteria for function as an aposematic cue, a signal should be conspicuous, it must be unambiguously associated with the communicator, and there must be a potential cost to the recipient of the signal.

Greene (1973) categorized defensive tail displays of snakes into three major functions: 1) to divert attack toward the tail, 2) to inhibit attack with an aposematic display, and 3) to disorient the predator with a flash

display. Certainly, these functions are not entirely mutually exclusive. The behavior scores from CCA I indicated that the four large-bodied rattlesnake species in my study presented a conspicuous, potentially aposematic signal with noticeably louder sound produced by their rattles and enhanced showiness through elevation of their tails and positioning them more centered on their bodies. The aposematic tail display in large-bodied rattlesnakes may also function as a diversion since head hiding was very closely associated with tail elevating. In contrast, the small-bodied rattlesnakes produced barely audible rattling sounds and elevated their tails much less than their larger counterparts. Small-bodied rattlesnakes and non-rattlesnakes alike positioned their tails more distal or more proximal to the predator, and hid their tails more often - certainly not characteristic of a conspicuous aposematic signal. Thus, I conclude that the function in smaller snakes is distraction. Given the phylogeny of the species in my study, the use of the tail as a distraction appears to be the ancestral character state. Tail vibration itself, as a distraction away from the head, is also a plesiomorphic character for pitvipers as indicated by CCA I. This is also supported by the fact that tail vibration is common among non-venomous taxa as well

(Greene, 1994a). However, it is safe to assume that a tail with a rattle, even a small one, would make more noise than a tail without a rattle, and thus, be a better distraction. This is all that would be required for the evolution of the rattle as an enhancement for caudal distraction.

Large rattlesnakes pose a substantially greater threat than do smaller rattlesnakes because the former potentially deliver more venom (Hayes, 1991) and more effective strikes, strike speeds, and strike distances (Row and Owings, 1990). Body size and temperature, as opposed to interspecific differences, account for most of the variation in the acoustical properties of rattling (with the exception of *S. miliarius*, which has a disproportionately small and quiet rattle) (Fenton and Licht, 1990; Cook et al., 1994; Young and Brown, 1995). Adult ground squirrels (*Spermophilus beecheyi*), which have some immunity to the bite of northern Pacific rattlesnakes (*Crotalus viridis*), have been known to kill rattlesnakes and even engage in probing behavior to elicit a snake to rattle apparently because this provides information about the relative danger of an individual snake (Rowe and Owings, 1996). It is safe to assume that snake predators might make similar assessments.

Hence, it does not appear that rattling and use of the tail by smaller rattlesnakes fit the criteria of an aposematic cue, at least in the context of my artificial predator. Greene (1994a) proposed that the rattle of smaller rattlesnakes might have evolved to signal (warn) small vertebrate predators. However, no ultrasonic or high-energy wavelengths in rattle sound production have been detected (Fenton and Licht, 1990; Cook et al., 1994) to suggest that there is a sound produced beyond the range of human hearing that could be detected only by smaller predators. Plus, these small-bodied rattlesnakes did rattle their tails when threatened by my (artificial) medium to large-sized predator.

It appears then that the evolution of the rattle and its use as an aposematic signal may be functionally constrained by body size. Smaller rattlesnake species retain plesiomorphic antipredator behavior in which the advent of a rattle merely accentuated the use of the tail as a distraction away from the head. The use of the tail as an aposematic signal could not evolve, since these smaller snakes pose a less substantial cost, relative to larger snakes, for potential predators. Use of the rattle as an aposematic signal apparently coevolved with body size in large-bodied rattlesnake species.

Ultimate and proximate determinants

After removal of the effects of phylogeny (CCA II), none of the other ultimate factors (e.g., presence or absence of a rattle) helped to explain the remaining variation in antipredator behavior. Although sex was correlated with certain behavior patterns (males having more passive defense than females), this appeared to be an artifact of sexual dimorphism in body size and had no explanatory value by itself. The important proximate factors were body temperature, reproductive stage, evidence of previous injury, and ontogenetic growth stage as indexed by snout-vent length (Figure 16).

My results showed no positive or negative relationship between striking behavior and body temperature. However, there was a temperature-dependent response in other behavior patterns, in that warmer snakes had less protected body postures, escaped more lateral to the predator, and presented less aposematic tail and mouth displays than cooler snakes. Previous studies on snakes (mostly garter snakes, *Thamnophis* spp.) are contradictory in this respect. The majority of work has used strike behavior as an index for active defensive behavior and indicates that colder snakes are more likely to use more active antipredator defense (Fitch, 1965; Heckrotte, 1967; Arnold and Bennett,

1984; Costanzo, 1986; Passek and Gillingham, 1997; Shine et al., 2000). However, Schieffelin and de Quieroz (1991) and Keogh and Deserto (1994) found the opposite. My research corroborates the results of the majority of past studies: warmer snakes in my study had a more passive antipredator behavior complex in that they were less apt to elevate or rattle their tails, exhibited more open posterior bodies, and escaped directionally more lateral to the predator as opposed to away or toward the predator. This is the first strong evidence of general temperature-dependent antipredator behavior in non-colubrids. Goode and Duvall (1989) found temperature dependence in antipredator behavior only in gravid female prairie rattlesnakes, *C. viridis*.

To explain this inverse relationship between active antipredator defense and body temperature, I turn to an optimality model as the best explanation of biological significance (Shine et al., 2000). Since warmer body temperatures afford snakes better capacity for locomotor performance, warmer snakes may have no need for active displays and defense; they can rely more on escape than confrontation. In terms of escape direction, the backward crawl is slow and escape toward a predator is more risky, making lateral escape the best alternative.

Reproductive status (i.e., gravid females) affected antipredator behavior much in the same way as higher body temperatures, except that it was additionally associated (negatively) with the frequency of open-mouth strikes in gravid females. Two previous studies found significant interactions between gravid females and body temperature with respect to defensive behavior in prairie rattlesnakes, *C. viridis* (Goode and Duvall, 1989; Kissner et al., 1997). Both studies measured the duration to strike at an approaching predator (human), but they differed in results, one finding that cooler gravid females were more active in their antipredator defense (Goode and Duvall, 1989) and the other finding that such females were more passive (Kissnerr, et al., 1997). My observations differ methodologically since I dealt only with post-detection antipredator behavior. Upon first inspection, my findings agree with Goode and Duvall (1989). However, a functional interaction of these two factors is doubtful since snakes were not allowed to self-thermoregulate prior to the trials in my study, suggesting that this is not a true interaction, but rather a convergence of similar antipredator behavior between warm snakes and gravid snakes. To test this idea, I performed a Kruskal-Wallis One-Way Analysis of Variance on body temperature of gravid

females ($n = 28$) vs non-gravid females and males ($n = 149$). There was no significant difference ($p > 0.05$) in body temperature and, in fact, non-gravid females and males had nominally higher body temperatures ($\bar{x} = 26.8$ degrees Celsius) than did gravid females ($\bar{x} = 25.8$ degrees Celsius). The convergence in antipredator behavior of gravid snakes with warmer snakes is puzzling since it is counter to the optimality model I used to rationalize this behavior in warmer snakes; gravid females, unlike warmer snakes, have reduced locomotor capabilities (Siegel et al., 1987). It may be that since gravid snakes in the field maintain higher body temperatures than males and non-gravid females, they are "hardwired" to perform as though they are indeed at those higher temperatures even when they are not. An alternative hypothesis is that being gravid more severely constrains a snake's ability to physically perform active defense than to escape by fast locomotion, so a gravid female has no choice but to flee. Instead of an active defense, a gravid female before flight may rely on more passive defensive behavior, such as chemical defense (see tail rubbing behavior, below). This conundrum offers an opportunity for research into constraints of body temperature and reproductive condition on snake antipredator behavior.

Tail rubbing, a behavior found only in large-bodied rattlesnakes, was mostly performed by gravid females. This behavior is associated with cloacal sac discharge and its function appears to be to spread exudates over the body of the snake. Such secretions may serve as a noxious defense to deter predators (Klauber, 1972; Price and LaPointe, 1981). There is also evidence that alarm pheromones found in the discharge might serve to warn conspecifics of a predator threat (Graves and Duvall, 1988), parallel to the *shreckstoff* (Mathis and Smith, 1993) found in fishes and chemical communication of stress found in larval salamanders and tadpoles (Lutterschmidt et al., 1995). It is well known that gravid females aggregate at suitable basking sites to maintain elevated body temperatures. While both male and female rattlesnakes in temperate climates den communally, they are congregated only for a short time after emergence in the spring; afterward, males and non-gravid females disperse. Gravid females remain closer to the den site until parturition. If, as it has been proposed (Goode and Duvall, 1989), kin selection has led to the evolution of a conspecific alarm signal, it seems most likely among the aggregated gravid females. My observed correlation of tail rubbing behavior with gravid females suggests this might be the case.

Of all the proximate independent variables, evidence of previous injury is the one most likely to be influenced by learning or altered due to previous experience. Since previously injured snakes behaved in the same manner as gravid females and warm snakes, it may be that they were less willing to proactively engage the enemy. As the ditty goes, "Once bitten, twice shy." In my study, it is impossible to determine if this learning represents an altered behavioral decision due to a snake's ability to evaluate and thus, better respond to a predator, or simply a habituated reduction in active behavior due to stress. Herzog et al. (1989) found evidence of short-term habituation of antipredator behavior in garter snakes with decreased escape and striking behavior exhibited toward repeated threat stimuli. While the extent of long-term effects of stressful encounters in pitvipers is not known, there may be hormone-mediated reduction in aggressive behavior. Schuett and Grober (2000) found that post-fight levels of corticosterone in losers of male-male intraspecific encounters had a negative effect on metabolic recovery, suggesting protracted inhibitory effects. Regardless of mechanism, the question of whether this reduction in active antipredator behavior results in increased fitness needs further study.

An alternative explanation is that snakes that for one reason or another were more passive in their antipredator behavior sustained more injuries, not that previously injured snakes became more passive. This is certainly a possibility, but I cannot address it with my data because I measured each individual snake only once.

In CCA II, after removing the effects of phylogeny, larger snakes (or ontogenetically advanced snakes) exhibited fewer open-mouth strikes, had more coiled body postures with their heads often hidden and positioned centered on their bodies or distal to the predator, and gave more aposematic displays such as mouth gape, elevated tail, and tail wriggling compared with smaller snakes. This proximate relationship between snout-vent length (as ontogenetic growth stage) and antipredator behavior mimics the relationship of species-specific body size (as an ultimate determinant) and antipredator behavior, where small body size represents a functional constraint on the use of aposematic signals. Smaller snakes, regardless of species, have no choice when confronted by a predator but to strike with less efficient venom delivery systems and engage the predator more actively, not being able to coil up into a defensive posture and withstand a brief attack. Larger snakes have better venom delivery systems and can

first warn a predator. If the predator does not respond to the aposematic signal, they can deliver a few effective bites, then cover up their heads and withstand a brief attack while they wait for the envenomation to repel the attacker.

Finally, I point out that two ubiquitous and plesiomorphic behavior patterns that were not associated with ultimate factors in CCA I, tail vibration and open-mouth strike, were strongly associated with proximate factors in CCA II. This contrast demonstrates the value of integrating both ultimate and proximate determinants into experimental designs. My integrative approach allowed me to infer both "why" and "how" pitvipers exhibit specific antipredator behavior. Both ultimate and proximate factors have shaped the expression of antipredator behavior.

At the ultimate level of causation, I determined that pitvipers evolved species-specific modes of antipredator defense. More phylogenetically basal, small-bodied species of rattlesnakes were overall plesiomorphic in their antipredator behavior, indicating that no specialized behavior evolved concurrent with the earliest rattle. The evolution of an aposematic function for the rattle and associated stereotyped behavior such as the elevated S-coil

appears to be linked to the coevolution of increased body size in rattlesnakes.

At the proximate level, warmer snakes and gravid females were associated with generally more passive antipredator behavior. Larger individuals also displayed more passive defensive behavior, with the added use of aposematic signals.

Tail vibration and open-mouth strikes were ubiquitous and plesiomorphic across species at the ultimate level, but modulated by proximate factors. Small body size appears to be a functional constraint on the use of aposematic signals at both ultimate and proximate levels of causation.

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Table 1. Numbers of each species by sex, and snout-vent lengths for snakes used in antipredator trials.

Location	Species	SVL (mm)			N		
		Total	Males	Females	Mean	Min.	Max.
Arkansas	<i>Agkistrodon contortrix</i>	34	14	20	486	190	720
	<i>Agkistrodon piscivorous</i>	40	15	25	547	232	890
	<i>Crotalus horridus</i>	4	2	2	804	492	1023
	<i>Sistrurus miliarius</i>	8	1	7	348	202	425
Arizona	<i>Crotalus atrox</i>	31	13	18	667	245	1111
	<i>Crotalus molossus</i>	5	3	2	886	751	1030
	<i>Crotalus scutalatus</i>	40	20	20	431	223	812
	<i>Crotalus pricei</i>	2	1	1	263	271	255
	<i>Sistrurus catenatus</i>	7	5	2	349	279	400
Mexico	<i>Bothrops asper</i>	6	2	4	821	370	1652

Table 2. Catalog of observed antipredator behavior in pitvipers.

Head Elevation

- 1 HELEV - Head elevated above substrate
- 2 HDEPR - Head depressed onto substrate

Head Exposure

- 3 HHIDE - Head hidden from view
- 4 HPROT - Head protected
- 5 HEXPO - Head exposed and unprotected
- 6 HVEXP - Head ventral surface exposed

Head Orientation

- 7 HAWAY - Head facing away from predator
- 8 HLATR - Head oriented laterally to predator
- 9 HFACE - Head facing predator

Head Position

- 10 HCENB - Head centered on main mass of body
- 11 HDISB - Head positioned distal to the predator
- 12 HLATB - Head positioned lateral to the predator
- 13 HPROX - Head positioned proximal to the predator

Head Displays/Actions

- 14 MGAPE - Mouth gape
- 15 CSTRI - Closed mouth strike
- 16 OSTRI - Open mouth strike
- 17 LATHD - Lateral head display

Posterior Body Elevation

- 18 BPDEP - Posterior body depressed onto substrate
- 19 BPELE - Posterior body elevated above substrate

Table 2 continued...

Anterior Body Elevation

- 20 BADEP - Anterior body depressed onto substrate
- 21 BAELE - Anterior body elevated above substrate

Posterior Body Exposure

- 22 BPVEX - Posterior venter exposed

Anterior Body Exposure

- 23 BAVEX - Anterior venter exposed

Composite Body Postures

- 24 BASYM - Body in asymmetrical coil
- 25 BTCOI - Body in a tight coil
- 26 BLCOI - Body in a loose coil

Anterior Body Postures

- 27 BACOI - Anterior body coiled
- 28 BASIN - Anterior body postured sinusoidally
- 29 BASTR - Anterior body postured straight

Posterior Body Postures

- 30 BPCOI - Posterior body coiled
- 31 BPSIN - Posterior body postured sinusoidally
- 32 BPSTR - Posterior body postured straight

Body Actions

- 33 AESCA - Escape away from predator
- 34 LESCA - Escape lateral from predator
- 35 TESCA - Escape toward predator
- 36 STATI - Body stationary
- 37 BTHRO - Erratic body throw

Table 2 continued...

Tail Elevation

- 38 TDEPR - Tail depressed onto substrate
39 TELEV - Tail elevated off substrate

Tail Exposure

- 40 THIDD - Tail covered from view
41 TEXPO - Tail exposed to view
42 TVENT - Tail venter exposed

Tail Postures

- 43 TPROX - Tail positioned proximal to predator
44 TLATR - Tail positioned lateral to head
45 TDIST - Tail positioned distal to predator
46 TCENT - Tail centered on main mass of body

Tail Actions/Displays

- 47 TLRUB - Tail rubbed over body or head
48 TCOIL - Tail coiled/curled
49 TWRIG - Tail wriggled
50 TVIBR - Tail vibrated
-

Table 3. Eigenvalues, *F*-statistics,
and *p*-values for first four axes
from CCA I.

Axis	Eigenvalue	<i>F</i>	<i>p</i>
1	0.090	19.84	0.0003
2	0.024	6.80	0.0003
3	0.018	5.23	0.0020
4	0.016	5.32	0.0020

Table 4. Behavior scores for first four axes in CCA I (positive and negative scores that are explained best by each axis).

Axis One				Axis Two				Axis Three				*Axis Four	
Pos. Scores		Neg. Scores		Pos. Scores		Neg. Scores		Pos. Scores		Neg. Scores		Pos. Scores	
TESCA	1.19	TELEV	-1.60	TTHRA	2.36	BPSTR	-1.51	BASYC	3.87	MGAPE	-1.94	HDEPR	0.27
BASTR	0.96	HHIDE	-1.53	BTCOI	0.77	HLATE	-0.58	THIDD	1.02	TLRUB	-1.15	TPROX	0.34
HEXPO	0.84	TCENT	-1.17	TVIBR	0.24	HPROB	-0.54			LESCA	-0.61	HDISB	0.41
TDEPR	0.71	BAELE	-0.96			OSTRI	-0.26					TVENT	6.11
TDIST	0.68	HCENB	-0.94			TLATR	-0.25					TCOIL	6.14
BASIN	0.62	BLCOI	-0.78			HELEV	-0.14						
HAWAY	0.48	BPCOI	-0.70			TEXPO	-0.10						
HLATB	0.45	BACOI	-0.63			BPDEP	-0.06						
BPSIN	0.42	AESCA	-0.61										
BADEP	0.39	HPROT	-0.35										
STATI	0.31	HFACE	-0.28										
		TVIBR	-0.24										

*There were no negative scores for axis four.

Table 5. Eigenvalues, *F*-statistics,
and *p*-values for first four axes
from CCA II.

Axis	Eigenvalue	<i>F</i>	<i>p</i>
1	0.020	4.64	0.001
2	0.013	3.79	0.011
3	0.008	2.85	0.083
4	0.005	2.16	0.504

Table 6. Behavior scores for first two axes in CCA II (positive and negative scores that are explained best by each axis).

Axis One				Axis Two			
Pos. Scores		Neg. Scores		Pos. Scores		Neg. Scores	
TLRUB	3.22	TELEV	-0.75	BPSTR	1.37	TWRIG	-0.89
LESCA	0.41	TESCA	-0.71	BASTR	0.92	BTCOI	-0.66
TDEPR	0.34	TVIBR	-0.46	THIDD	0.88	HCENB	-0.65
HDEPR	0.27	AESCA	-0.46	OSTRI	0.78	MGAPE	-0.60
TPROX	0.24	BLCOI	-0.38	HPROB	0.76	BAELE	-0.52
STATI	0.20	HPROT	-0.18	TDIST	0.64	BPCOI	-0.43
HAWAY	0.12	HELEV	-0.10	BASIN	0.29	TCENT	-0.33
BPDEP	0.02	TLATR	-0.09	HEXPO	0.29	HDISB	-0.30
				BPSIN	0.22	BACOI	-0.30
				BADEP	0.22	TEXPO	-0.04
				HLATE	0.17	HFACE	-0.03
				HLATB	0.02		

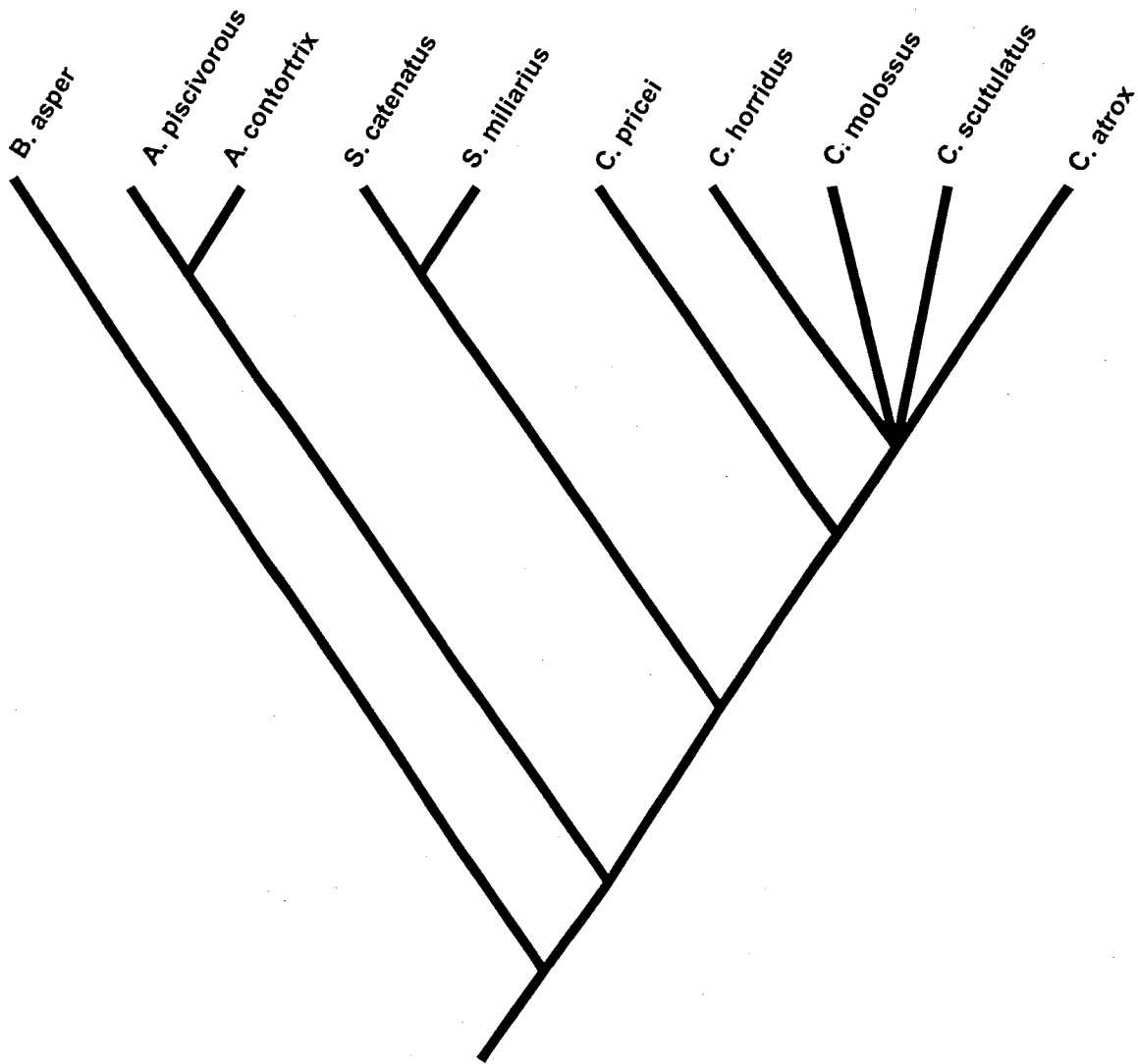


Figure 1. Phylogenetic hypothesis of pitvipers in this study as determined from Gloyd (1940), Brattstrom (1964), Klauber (1972a), Foote and MacMahon (1977), Stille, (1987), Knight et al., (1993), Parkinson, (1999), Parkinson et al., (2000), Bushar et al., (2001), and Murphy, et al., (in press).

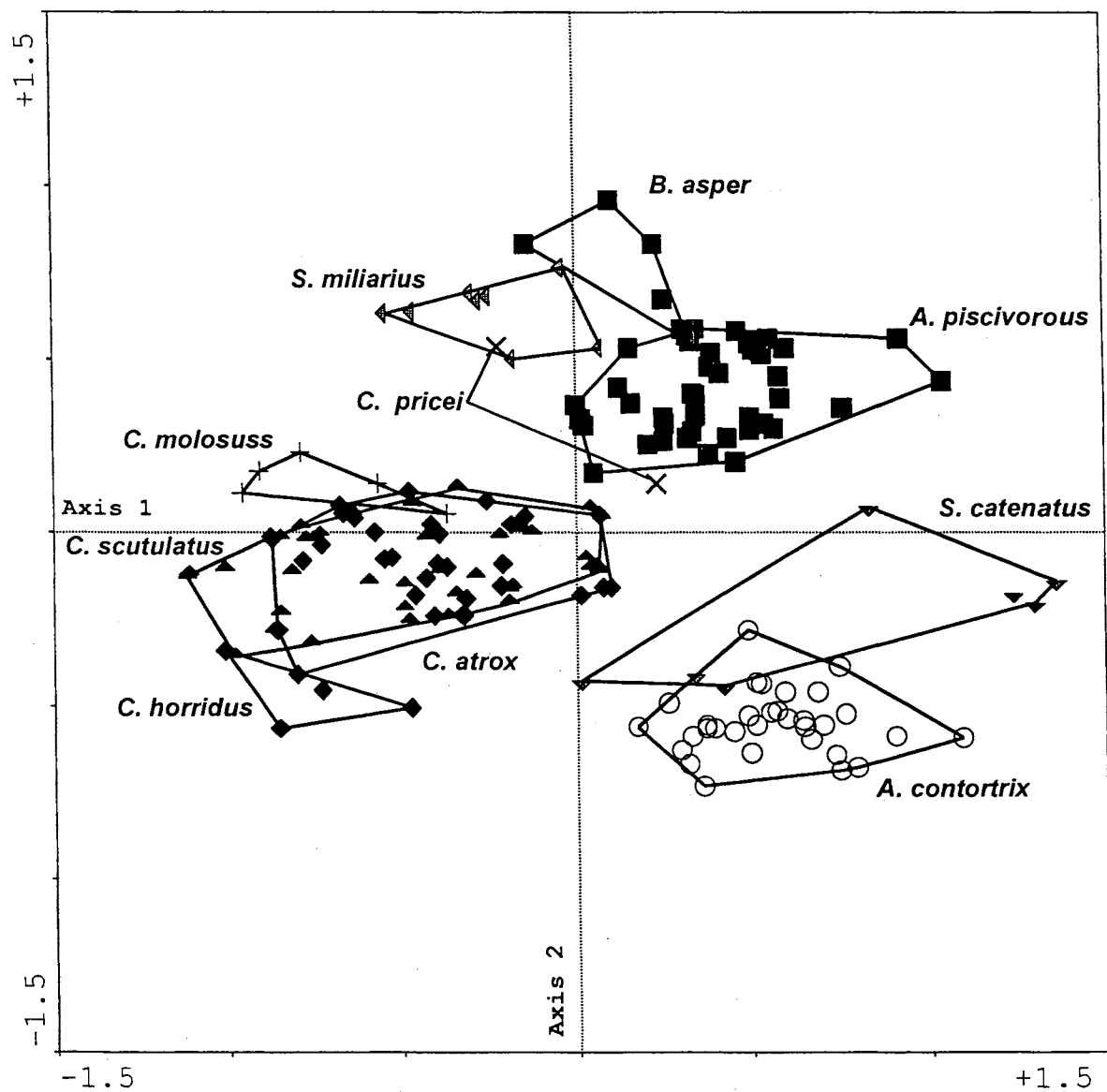


Figure 2. Snake scores for axes 1 & 2 in CCA I enclosed by minimum convex polygons by species.

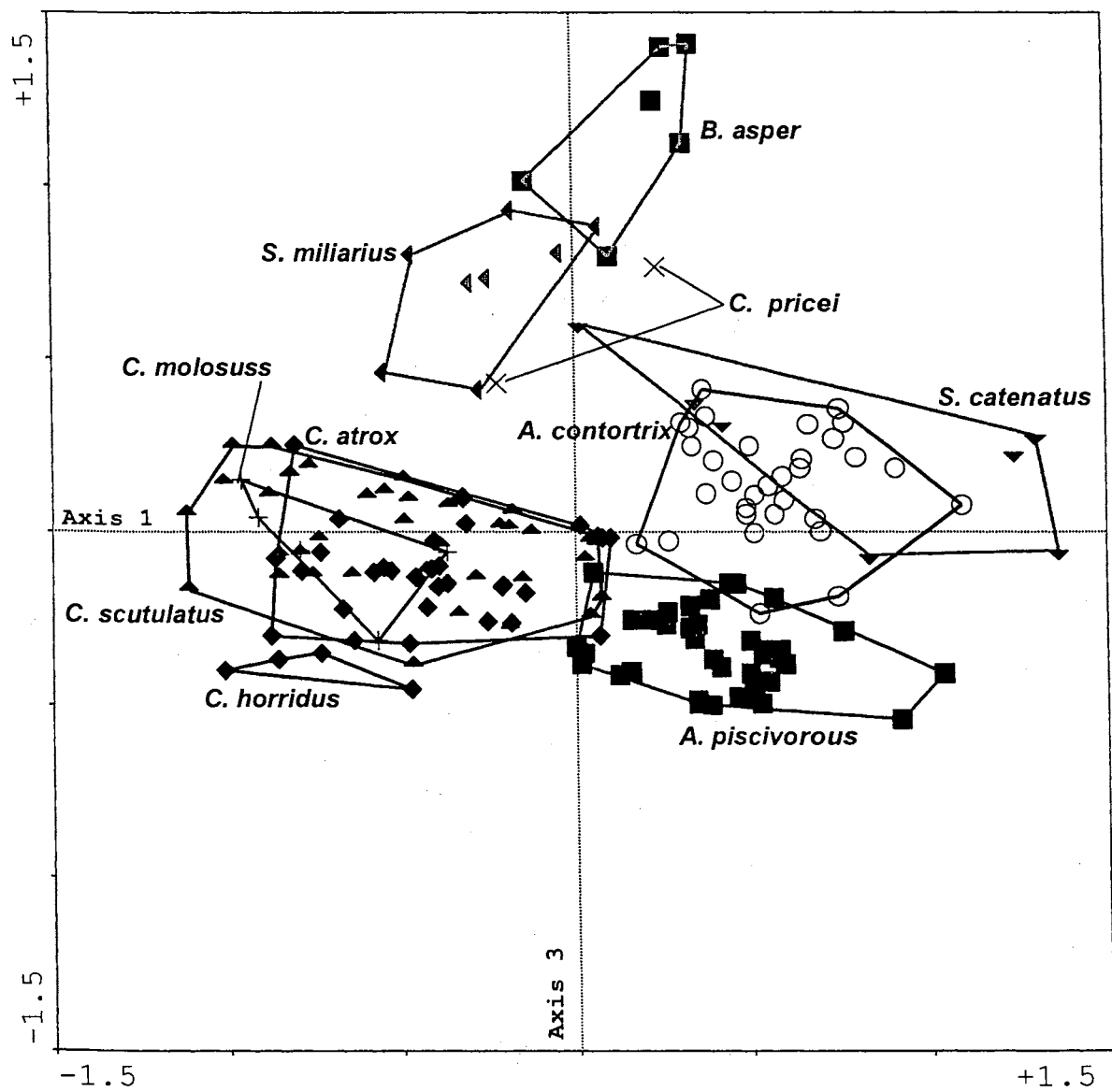


Figure 3. Snake scores for axes 1 & 3 in CCA I enclosed by minimum convex polygons by species.

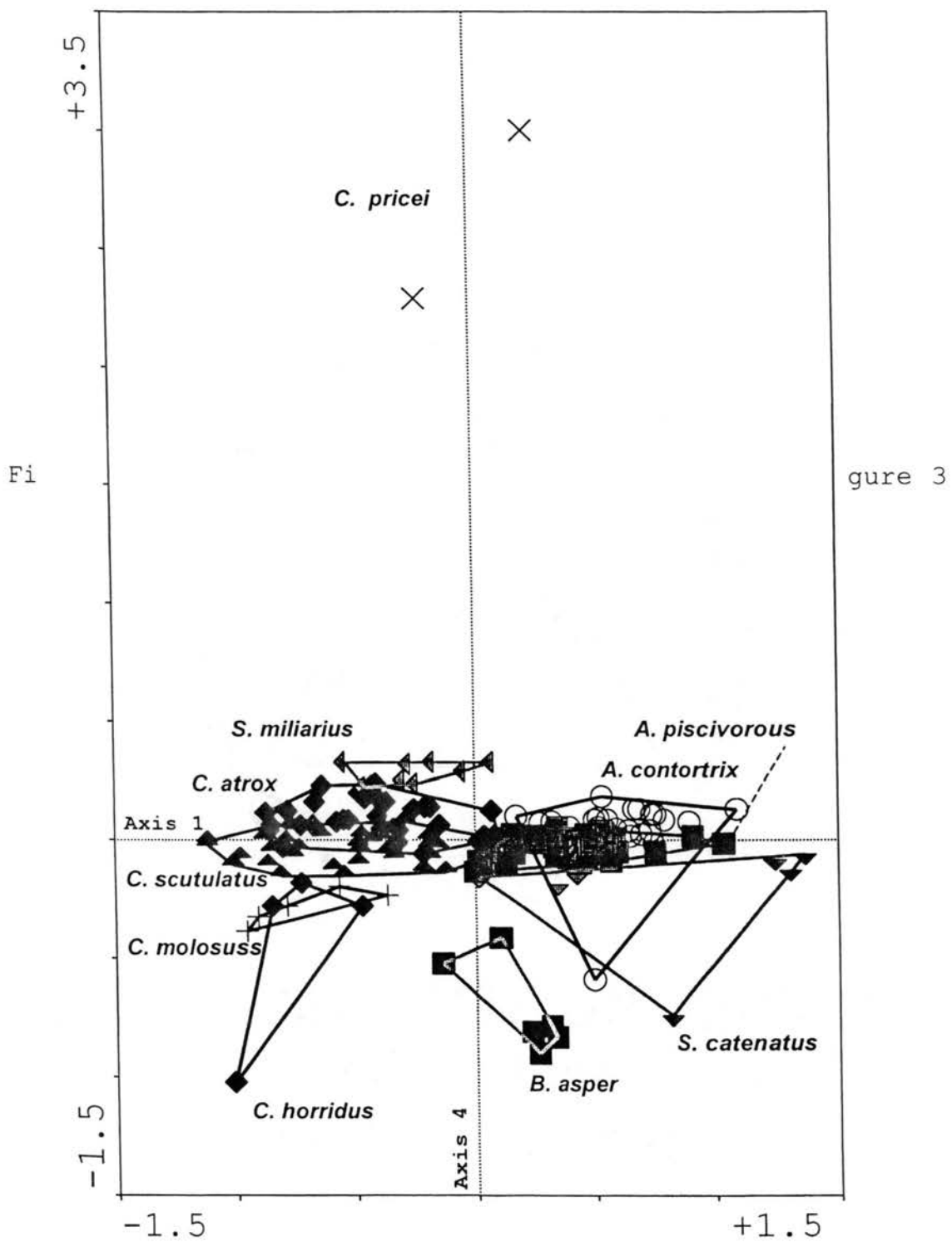


Figure 4. Snake scores for axes 1 & 4 in CCA I enclosed by minimum convex polygons by species.

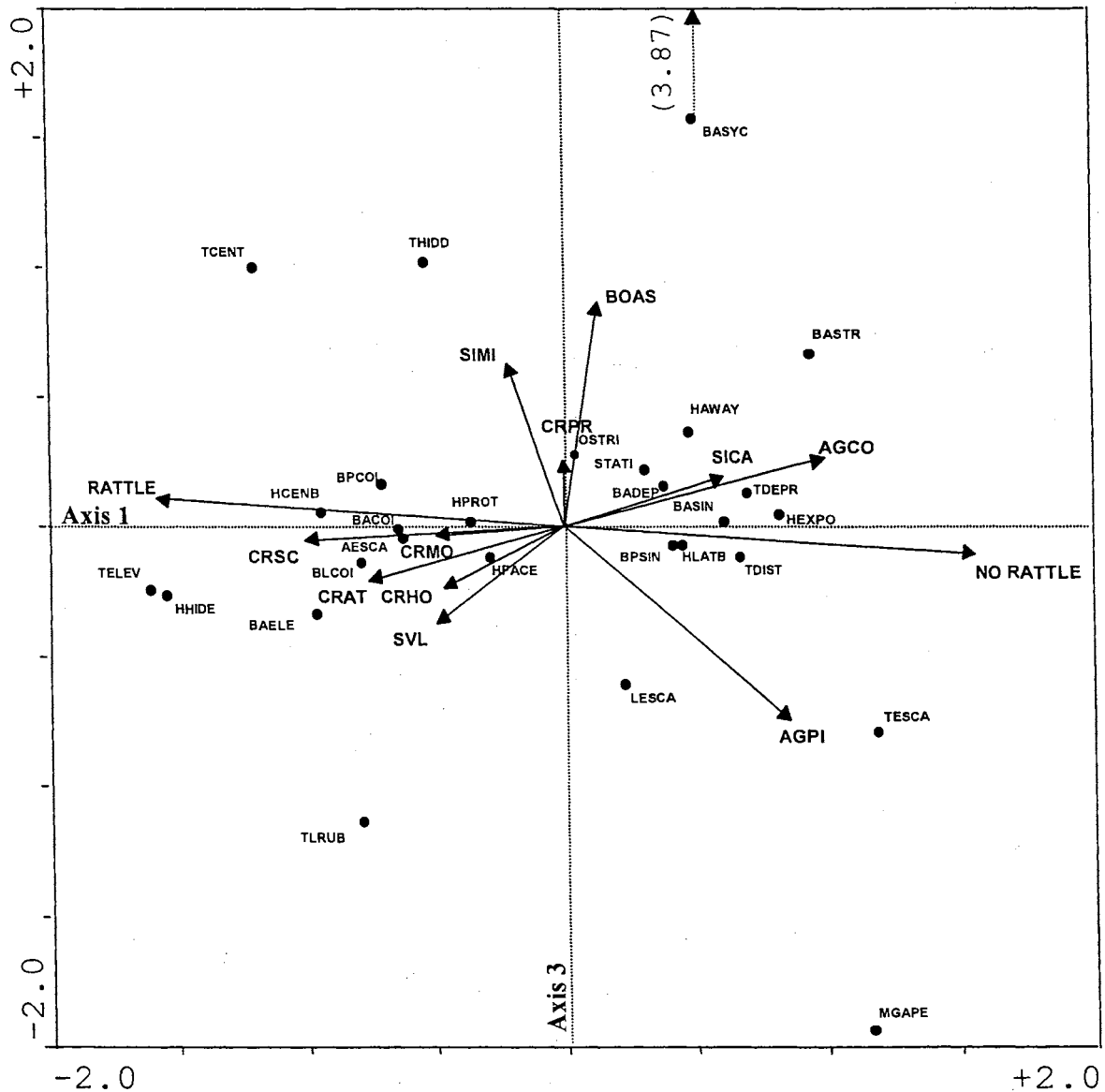


Figure 6. Behavior scores and vectors of ultimate independent variables (RATTLE, NO RATTLE, and SVL) for axes 1 & 3 in CCA I. AGCO = *A. contortrix*, AGPI = *A. piscivorous*, BOAS = *B. asper*, CRAT = *C. atrox*, CRHO = *C. horridus*, CRMO = *C. molossus*, CRPR = *C. pricei*, CRSC = *C. scutalatus*, SICA = *S. catenatus*, and SIMI = *S. miliaris*. Refer to Table 2 for behavior codes.

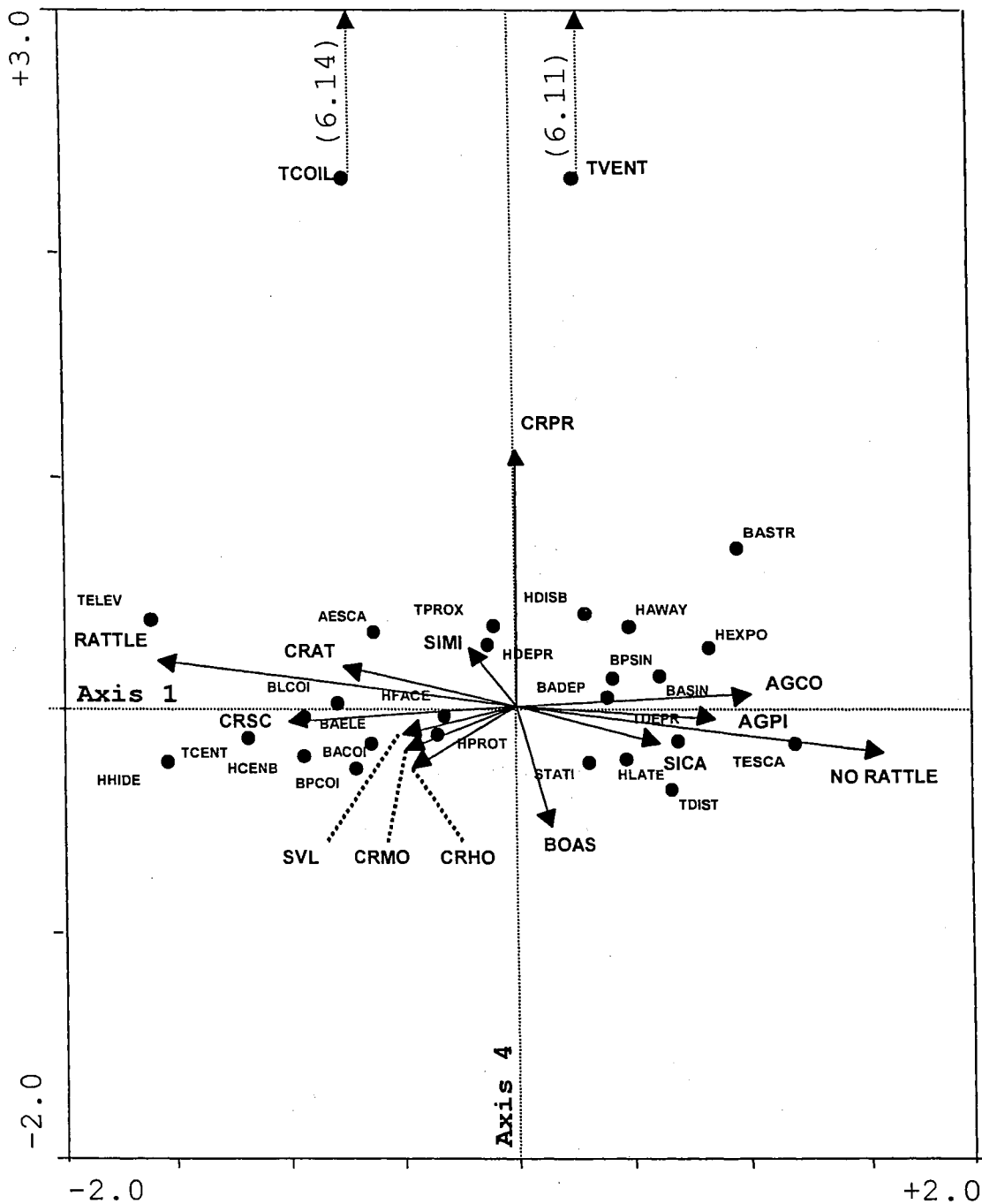


Figure 7. Behavior scores and vectors of ultimate independent variables (RATTLE, NO RATTLE, and SVL) for axes 1 & 4 in CCA I. AGCO = *A. contortrix*, AGPI = *A. piscivorous*, BOAS = *B. asper*, CRAT = *C. atrox*, CRHO = *C. horridus*, CRMO = *C. molossus*, CRPR = *C. pricei*, CRSC = *C. scutalatus*, SICA = *S. catenatus*, and SIMI = *S. miliaris*. Refer to Table 2 for behavior codes.

HEAD ORIENTATION

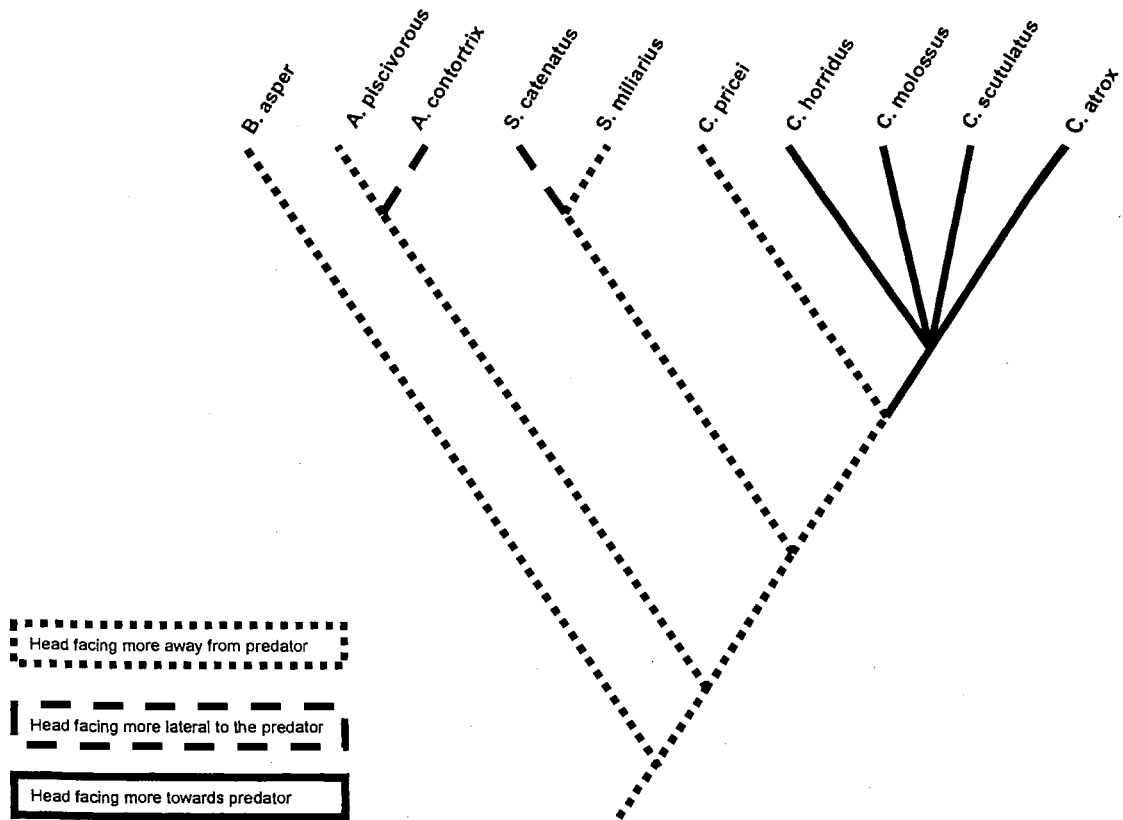


Figure 8. Evolution of head orientation in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

HEAD POSITION

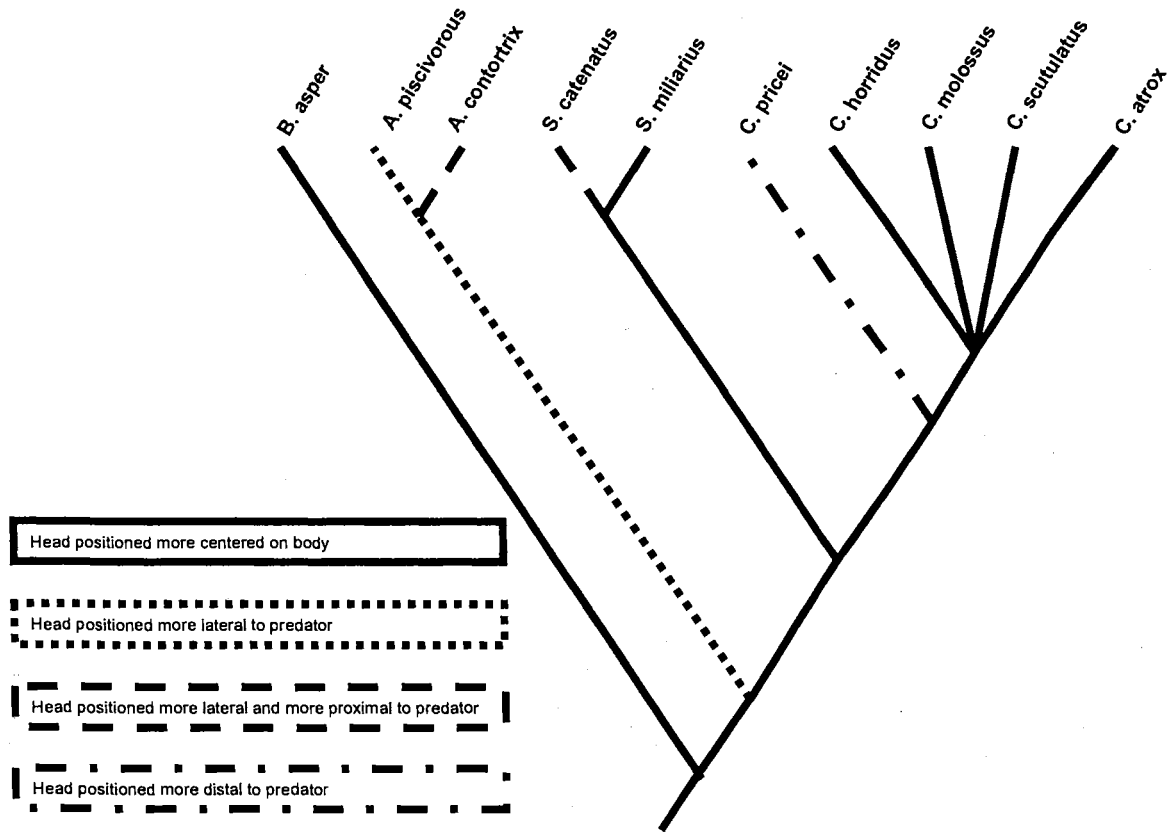


Figure 9. Evolution of head position in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

ANTERIOR BODY ELEVATION

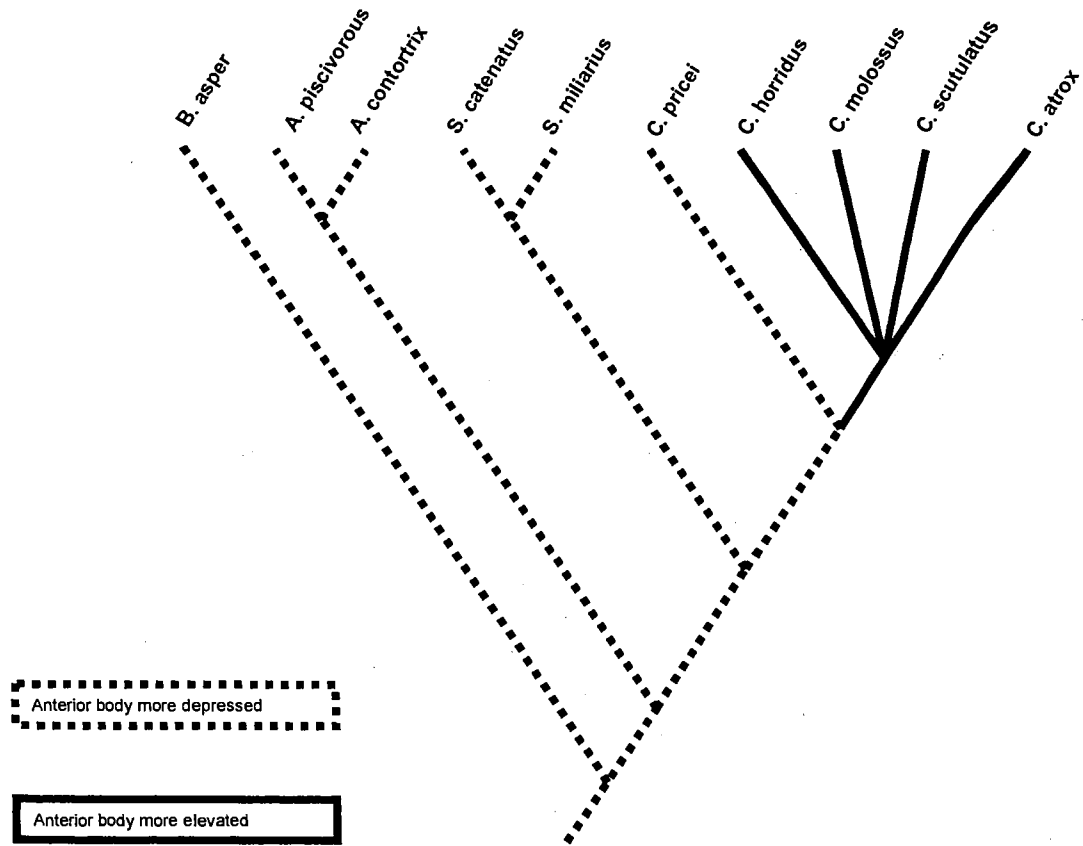


Figure 10. Evolution of anterior body elevation in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

OVERALL BODY POSTURE

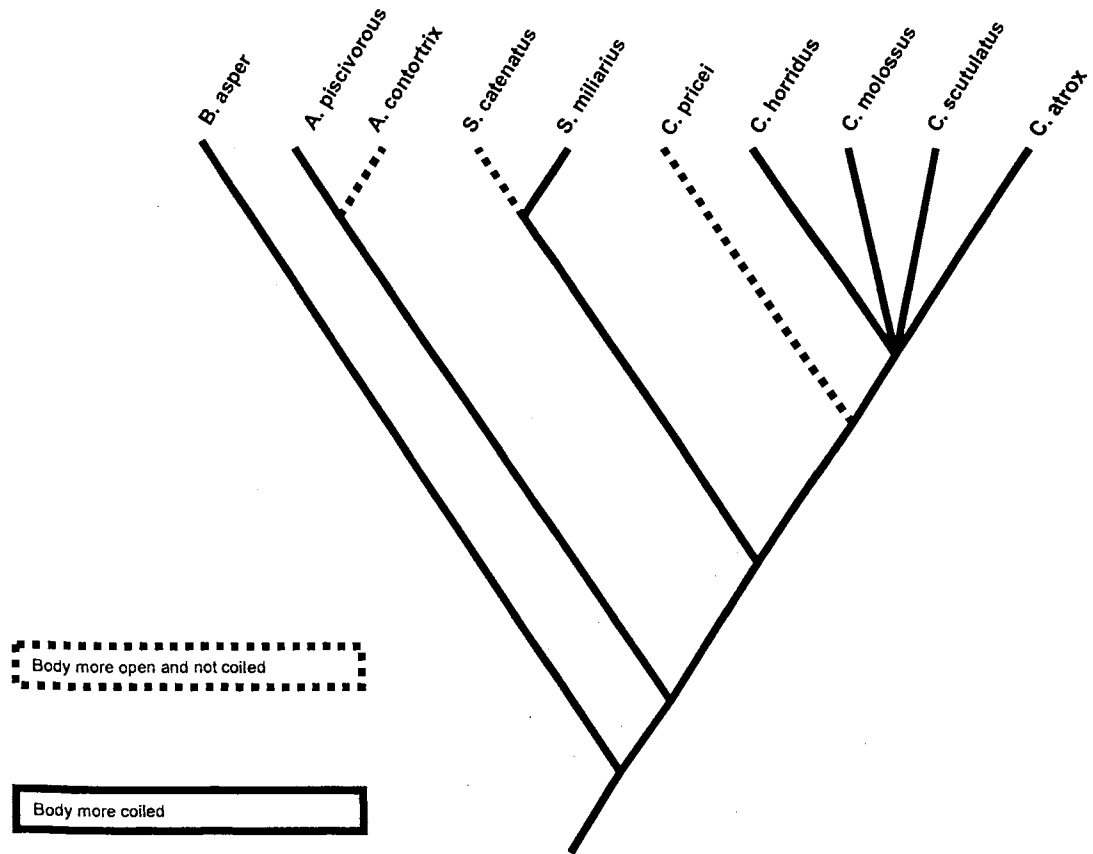


Figure 11. Evolution of overall body posture in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

TAIL ELEVATION

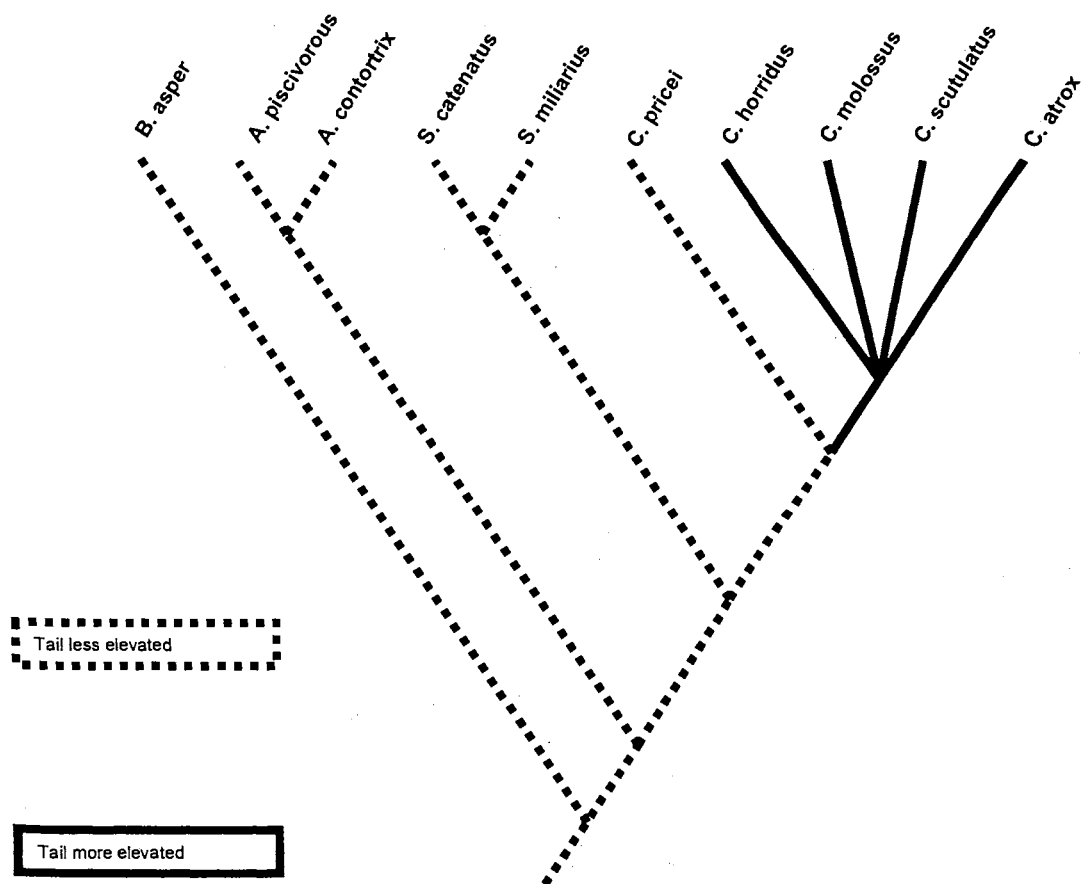


Figure 12. Evolution of tail elevation in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

TAIL EXPOSURE

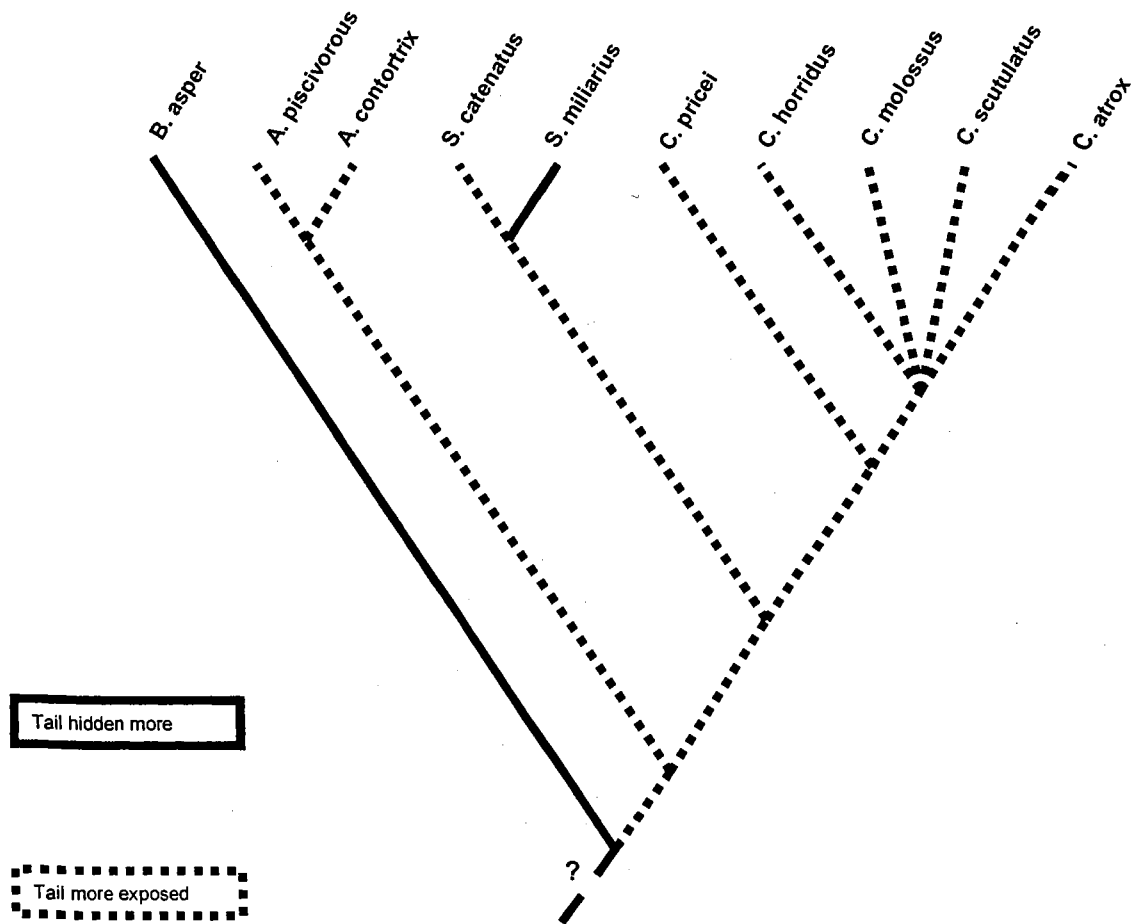


Figure 13. Evolution of tail exposure in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

TAIL POSITION

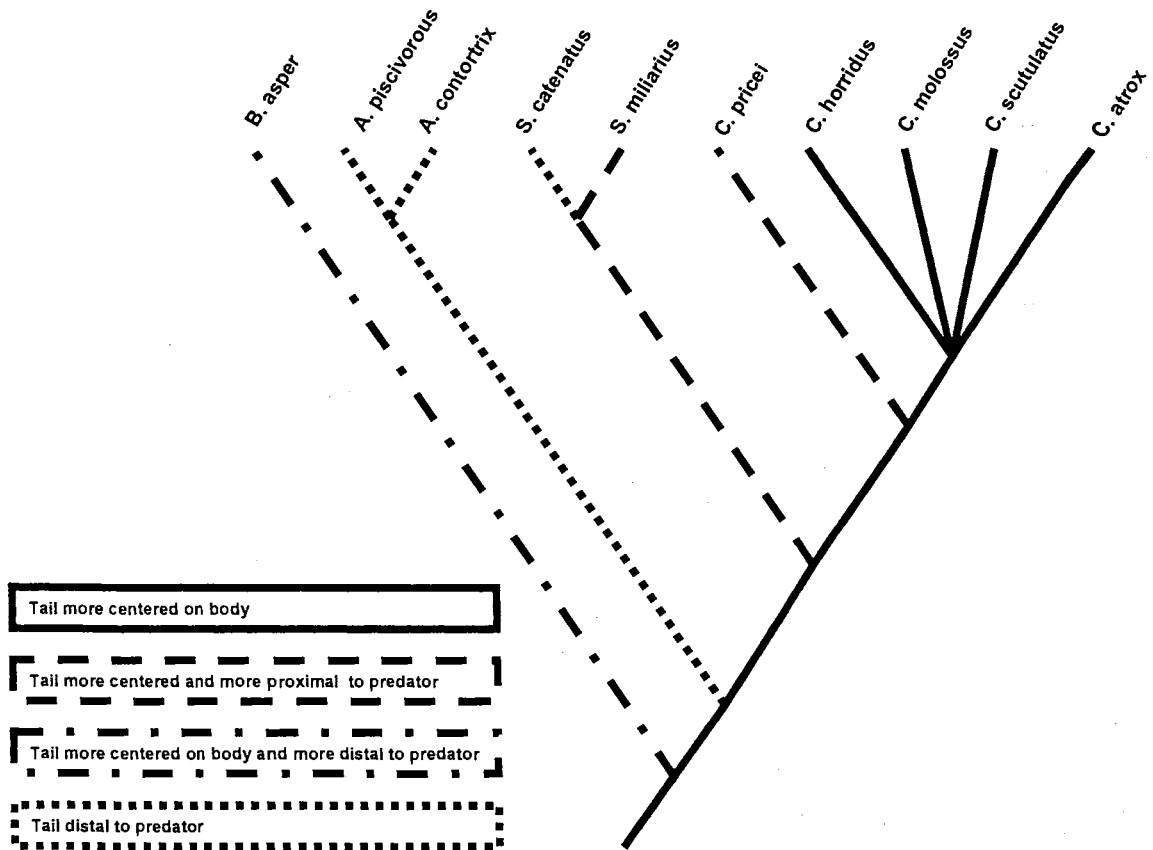


Figure 14. Evolution of tail position in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

ESCAPE DIRECTION

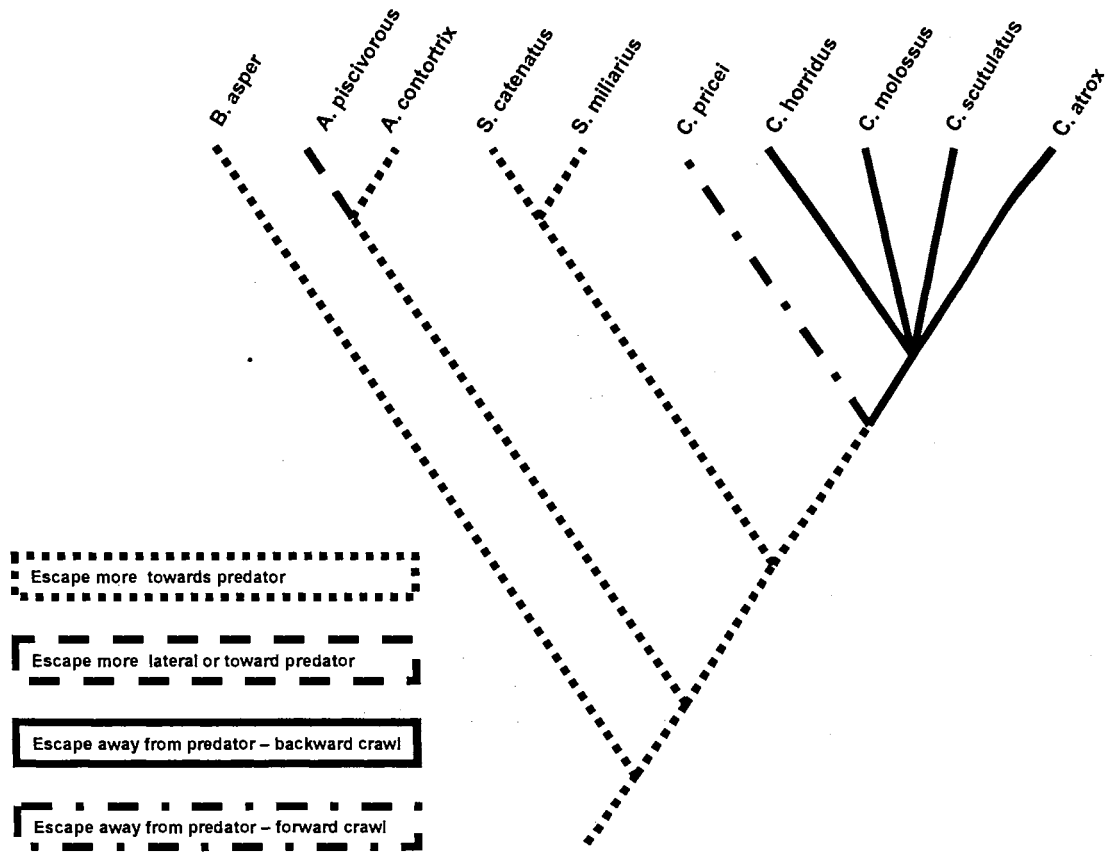


Figure 15. Evolution of escape direction in pitvipers. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

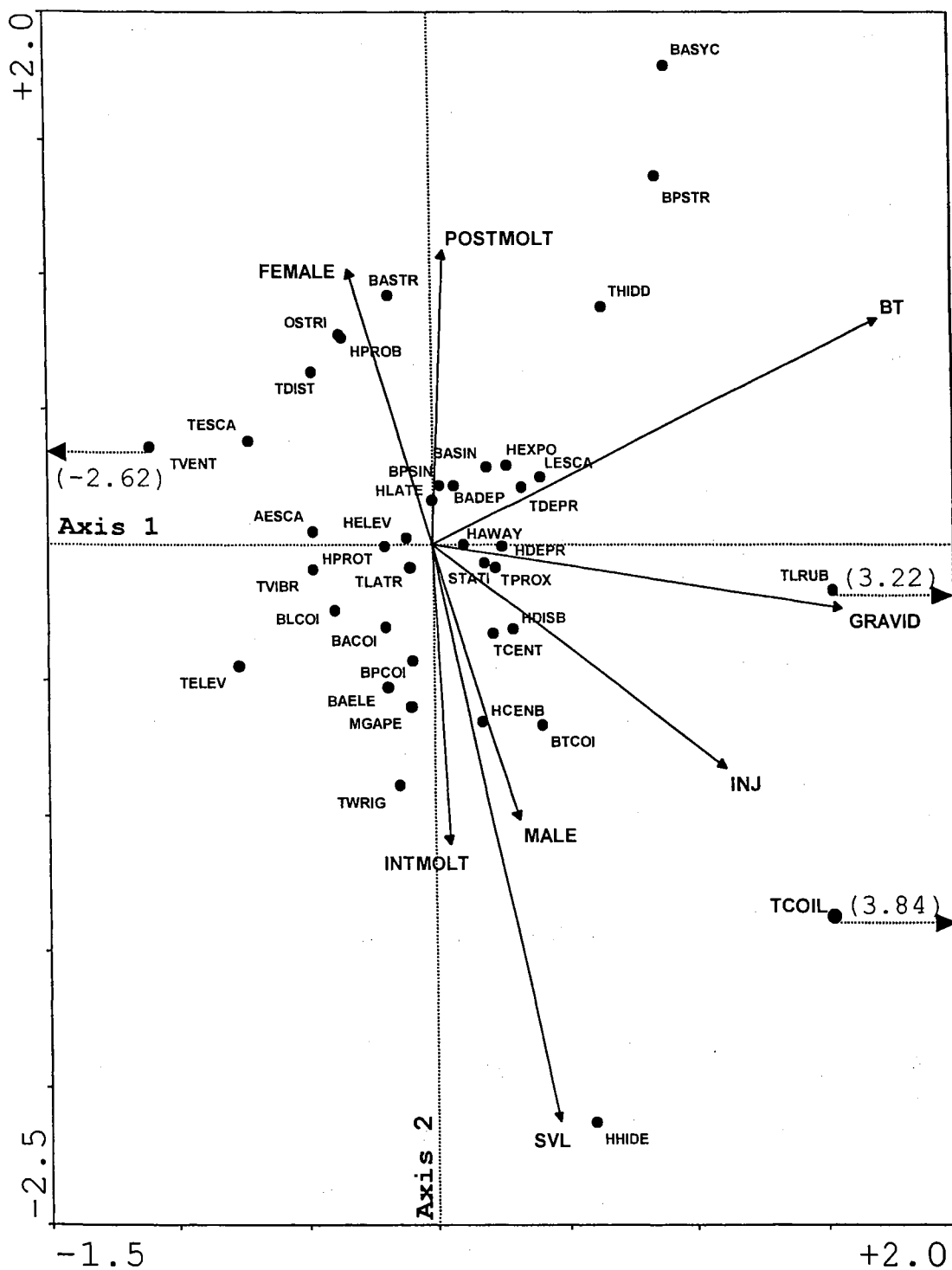


Figure 16. Behavior scores and vectors of proximate independent variables (FEMALE, MALE, SVL, GRAVID, POSTMOLT = post-molt stage of ecdysis, INTMOLT = intermolt stage of ecdysis, BT = body temperature, and INJ = evidence of previous injury) for axes 1 & 2 in CCA II.

THE EVOLUTION OF ANTIPREDATOR BEHAVIOR IN COLUBRIDS:
ULTIMATE AND PROXIMATE DETERMINANTS

Behavioral adaptations to predation in squamates range from avoidance tactics such as locomotor escape (Greene, 1994; Zug et al., 2001), cryptic locomotion patterns (Greene, 1994; Fleishman, 1985), differing degrees of wariness (Snell et al., 1988) and shifted times of activity (Fox, 1978) to specialized and stereotyped behavior such as elaborate tail displays (Green, 1973), postures (Greene, 1994), and sounds (Greene, 1992). Morphological adaptations include cryptic (Sweet, 1985) as well as brilliant coloration (Smith and Mostrom, 1985) and specialized structures such as the skeletal, vascular, and muscular arrangement found in lizards that have true tail autotomy - behaviorally controlled tail-loss (Bellairs and Bryant, 1985).

The causes and predictors of variation in antipredator behavior have been attributed to both ultimate and proximate factors. Most studies have focused on either quantified proximate causes with little or no reference toward ultimate factors or vice versa, giving unequal weight or bias to those primary factors being considered.

In lizards, antipredator tactics have been reported to be related to several influential factors: age and

nutrition (Stamps, 1983; Daniels, 1984); color pattern (Cooper and Vitt, 1985; Baird et al, 1997); geographical variation (Medel et al., 1990); habitat (Brattstrom, 1982; Daniels and Heatwole, 1990); morphology (Vitt and Congdon, 1978; Daniels et al., 1986; Sherbrooke, 1987); predation pressure (Shaffer, 1978; Schall and Pianka, 1980; Turner et al., 1982; Medel et al., 1990; Fox et al. 1994, Fox and Shipman, in press); predator type (Sherbrooke, 1987, 1991; Medel et al., 1988); previous experience with predators (Marcellini and Jenssen, 1991); reproductive status and sexual differences (Brown and Ruby, 1977; Snell et al., 1988); concurrent social interactions (Cooper, in press); and temperature (Bustard, 1968; Daniels, 1984; Losos, 1988).

Despite their being limbless, snakes exhibit the most diverse antipredator behavior found among reptiles (Shine et al, 2000; Greene, 1994). This, ironically, may well be a result of the necessity for creative solutions (adaptations) to avoid predation in lieu of the more standard modes of predator escape afforded by limbs.

Most published information on antipredator tactics in snakes is based on single-species studies with the relatively abundant natricine colubrids, most notably, gartersnakes (Shine et al., 2000). Descriptions of

antipredator behavior in snakes, particularly tail displays (Greene, 1973, 1994a), are well documented. Specialized and stereotyped antipredator behavior in snakes includes death feigning, envenomation, cloacal popping, cloacal sac discharge (musk), coiled tail displays, S-coil defensive postures, body balling and other tightly coiled defensive postures, tail vibration, mouth hissing, and dermal sound production (Greene, 1994a).

Although herpetologists have long known that snakes often exhibit highly repeatable, stereotypic antipredator behavior, there has been no comparative study based on directly measured observations of such behavior. Greene (1979, 1994b) and Jackson et al. (1976) suggested broad generalized trends in the predictability of antipredator behavior in snakes, but they did not explicitly address the effects of phylogeny. Greene (1979) reported that fossorial and terrestrial snake taxa that were not necessarily closely related converged toward one pattern of tail and head displays, and arboreal and semi-arboreal snake taxa converged toward a different pattern. Greene (1994b) also compared open-mouth threat displays of viperids in a more updated phylogenetic context. Jackson et al. (1976) used multivariate techniques to identify behavioral-ecological variables that maximally

discriminated between morphological groups of snakes based upon dorsal pigmentation patterns. While comparative in nature, data were qualitative scorings of morphological and behavioral-ecological variables for all species of snakes north of Mexico and were taken from personal field observations and the literature. Behavioral variables were more important than habitat in distinguishing among dorsal pigmentation patterns.

Other studies of antipredator behavior in snakes have dealt with descriptions and, to a limited extent, factors correlating with antipredator behavior (Greene, 1973; Arnold and Bennett, 1984; Sweet, 1985; Golani and Kochva, 1988; Brodie, 1989; Herzog et al., 1989; Herzog and Schwartz, 1990; Schieffelin and de Queiroz, 1991; Brodie, 1992; Savage and Slowinski, 1992). All of these previous studies of antipredator behavior in snakes used very simple and easily observed behavior such as the number of open-mouth strikes, escape speed, escape direction, latency to strike, and latency to escape.

Factors shown to affect or correlate with antipredator behavior in snakes are habitat (Greene, 1979; Golani and Kochva, 1988; Duvall et al., 1985); morphology and color patterns (Greene, 1973; Jackson et al., 1976; Brodie, 1992); geographic variation (Sweet, 1985; Herzog and

Schwartz, 1990); ability of the snakes to see the eyes of a potential predator (Herzog and Bern, 1992; Greene, 1994a; Burger, 1998); movement and size of threat stimuli (Scudder and Chiszar, 1977; Herzog et al., 1989); incubation temperature (Burger, 1998); body temperature (Arnold and Bennett, 1984; Goode and Duvall, 1989; Schieffelin and De Queiroz, 1991); reproductive status (Graves, 1989); social context (Duvall et al., 1985; Graves and Duvall, 1988); interspecific differences (Brodie, 1989; Herzog et al., 1989); and phylogeny (Greene, 1979, 1994b).

The intercorrelation of ultimate (historical and evolutionary) and proximate (developmental and environmental) causes has confounded attempts to understand relationships between these factors and antipredator tactics of snakes. This is owing to the fact that causation in biological systems occurs simultaneously at different levels (Duvall and Beaupre, 1998).

Questions concerning the origin of biological diversity in physiological, morphological, and behavioral phenotypes are commonly framed at two conceptual levels, ultimate and proximate (Mayr, 1993). Ultimate questions ask *why* a group of organisms exhibit a particular trait or character and proximate questions are aimed at *how* those traits or characters are expressed during the lifetime of

an individual (Alcock, 1993). This current characterization of ultimate and proximate questions subsumes Tinbergen's (1963) four epistemological categories of causation (proximate), ontogeny (proximate), survival value (ultimate), and evolution (ultimate). In a logical fashion, the agents invoked to address these questions are referred to as ultimate and proximate causes. Ultimate causes include more distant evolutionary history (phylogeny) and the adaptive significance that led to the evolution of particular traits, and proximate causes are the more immediate causes and developmental controls of the expression of those traits.

Ultimate causes include factors such as evolutionary history (phylogeny), life history mode, sex, and morphological characters such as adult body size, color pattern, and special anatomical structures (e.g., tail spines). These are factors that *have brought about* or coevolved with adaptive behavior through past action of evolution and this behavior is now displayed by contemporary individuals that inherit these factors. Proximate causes include factors such as microhabitat, ontogeny, previous experience with predators, social context, reproductive stage, body temperature, and body condition (health, presence or absence of a food bolus,

stage of ecdysis, etc.). These are factors that *bring about* specific behavior, or elicit it, in contemporary individuals experiencing one state or another of these influences that change during an individual's lifetime.

A conceptual framework for addressing these problems using an integrative approach has existed since the time of Aristotle, was employed by Darwin, and reiterated more recently (1970 to present) by others (Duvall and Beaupre, 1998). However, this integrative approach is seldom put into practice because of the perceived difficulty and historical constraints of computational power. Recent technological advances and the development of new statistical approaches (Fox and Shipman, in press) has put this ideal approach within the grasp of researchers willing to accept a paradigm shift in the way that research is conducted (Duvall and Beaupre, 1998).

Specifically addressing the problems encountered in the study of snake antipredator behavior, a way to deal with the intercorrelation of ultimate and proximate factors would be to simultaneously measure these factors and attempt to partition out the relative amount of variation attributable to the separate effects. In the context of a comparative study, this approach would support broad, general inferences about the evolution of antipredator

behavior in snakes and the ultimate and proximate factors that influence it.

In such an approach, relationships among multiple ultimate and proximate factors and antipredator behavior are assumed to exist a priori. In other words, it is assumed that to some as yet unknown amount, factors such as phylogeny, sex, body size, body temperature, and body condition are related to specific types of antipredator behavior. The questions asked are not then primarily focused on asking *if* these relationships exist, but *why*, *how*, and *to what extent* these factors are related.

Addressing these questions requires 1) some knowledge of the phylogenetic relationships of the taxa being considered (derived from independent data), 2) observations of other ultimate factors and control and/or measurements of proximate factors, and 3) a method to quantify the antipredator behavior in a common currency.

Part of the frustration with conducting research on the antipredator behavior in snakes is due to the difficulty in collecting enough empirical data. This a problem inherent to snake studies due to the arduous task of obtaining suitable numbers of observations on often sparse and secretive populations of snakes, leading to a phenomenon referred to as "lizard envy" (Siegel, 1993). I

agree with Siegel (1993), who acknowledges these difficulties, but additionally argues that "lizard envy" results from "1) not recognizing the limitations of snakes for certain kinds of studies, 2) not using different and innovative techniques when it is apparent that traditional techniques are inadequate, 3) not properly matching question, study animal, and technique, and 4) not focusing on the aspects of snake biology that make them 'model' organisms for certain kinds of research."

Despite these limitations, snakes are, in various ways, ideal for studies of factors affecting antipredator behavior. Many aspects of snake behavior and morphology are no doubt primarily driven by the selective forces of predation, or the relative lack thereof, as suggested by the well-documented, diverse, and highly specialized antipredator behavior found among snakes.

In this paper, I present an integrative comparative study of antipredator behavior in 27 species of colubrids in 18 genera. My objectives were to 1) quantify the antipredator behavior of snakes of different species by exposing them to a standard, graded, threat stimulus, 2) determine the evolution and phylogenetic components of antipredator behavior, and 3) remove the effects of

phylogeny and test relationships between ultimate and proximate factors and antipredator behavior.

METHODS

Capture of snakes

My goal was to quantify the antipredator behavior of as many individuals and taxa as time and resources would permit. I made experimental observations of antipredator behavior on 329 colubrids of 27 species across 18 genera. I employed several techniques of capture with standard post-capture handling at three general geographic locations: southeastern Arizona, west-central Arkansas, and southern Mexico.

I made three separate 10-day field excursions to southeastern Arizona to collect data for this study (August and September, 1995, and August, 1996). I captured snakes primarily by road cruising between 1900 and 2400 hrs on a 25-km section of Highway 80, 45 miles north of the city of Douglas in Cochise County. This locality has been an excellent area to obtain snakes for study by other workers (Mendelson & Jennings 1992). The work at this locality yielded observations on a total of 61 snakes of eight species (Table 1).

From 1996 to 1997, I conducted trials on snakes captured during another unrelated research project. Snakes were collected during diurnal, visual plot surveys in the Ouachita Mountains, north of Hot Springs, Arkansas, in Garland and Perry Counties five times a year from May 1995 to March 1999: early May, late May, mid-June, early October, and early the following March. I made experimental observations on 149 snakes of 18 species during this work (Table 1).

In 1996 and 1997, I obtained snakes for study in central Oklahoma, Cleveland County, using five drift fences established for a separate amphibian and reptile population study at each of two locations near the city of Norman, Oklahoma. Each drift fence array consisted of 45 m of 1-m tall plastic fencing arranged in a "T" (each arm = 15 m). Each drift fence array was equipped with 12 aluminum screen funnel traps and four pitfall traps. Arrays were checked daily for periods throughout the main activity season for reptiles and amphibians (March - October). This locality produced observations on a total of 119 snakes of 15 species (Table 1).

Snakes were picked up by hand and then placed individually into clean cloth sacks. These sacks were laid into 30-gallon coolers with damp paper towels to prevent

dehydration and then transported to a convenient outdoor site where trials were conducted and body measurements were taken. While awaiting processing, the snakes were kept in their individual sacks in the shade in open coolers or on the substrate.

Experimental techniques

I recorded the proportion of time (in seconds) that individual snakes spent in specific postures or actions while exposed to a standardized threat stimulus. Usually within 24 hours, but never longer than five days after their capture, I allowed snakes to acclimate to ambient temperature before placing them individually into a shaded, portable 1-m x 1-m neutral arena in the field. I then used a standard threat stimulus (Scudder & Chiszar 1977; Herzog et al. 1989; Bowers et al. 1993) to begin the trials.

My standard threat stimulus was a set of snake tongs fitted with an effigy of a generalized canine predator head constructed of foam rubber, covered with lycra material, and equipped with hobby eye-buttons. The mouth was outlined with canid-style teeth constructed from dense foam rubber. My choice of predator stimulus was made to provide a controlled, standardized threat with which to assay behavior, thus precluding the use of live predators. It has been shown in previous studies with snakes and lizards

that the exact shape of a predator stimulus is largely insignificant; rather, the movements and elevation of the stimulus are most important (Bustard, 1979; Herzog et al., 1989; Shine et al., 2000). Harry Greene has achieved repeatable results by subjecting snakes to the threat of a rubber Bart Simpson doll fitted onto the end of snake tongs (personal communication). Several researchers have used the human hand as a predator stimulus (Shine et al., 2000) but this technique was not considered due to the concern for safety with venomous taxa also studied (Chapter 1), but not reported here.

Snakes were exposed only one time each to a 3.5 minute trial with the following sequence of escalating levels of threat: no threat, no visible predator or observer, duration = 30 seconds; potential threat, observer moves to the arena and visually orients to snake, duration = 30 seconds; pre-capture threat exposure, predator lowered into the arena and situated one body length (of the snake in the arena) away from the snake - lateral to the snake if snake not coiled and facing snake's head if snake coiled, duration = 30 seconds; predator threaten, predator model thrust toward the snake (but not touching) at a rate of one thrust per second, duration = 30 seconds; pre-capture predator touch, snake touched with predator model mid-body

at a rate of one touch per second, duration = 30 seconds; predator grasp, snake gently picked up and lifted 50 cm (half the distance to the top of the arena) into the air and then placed back down, duration = single event usually lasting three to five seconds; post-capture predator touch, as pre-capture predator touch, duration = the remainder of a 30-second period beginning at predator grasp, usually 27 - 25 seconds; post-capture predator exposed, predator model movement stopped, duration = 30 seconds. The timing of each threat stage was made with a multiple-alarm laboratory timer. I personally conducted all trials. Resulting behavioral responses were recorded with a Canon ES800 8-mm video camera that I held while conducting each trial. Video data collection began at the potential threat stage.

Snakes were removed from the arena at the termination of each trial. I recorded several parameters for each snake after each trial: body temperature (immediately recorded after the trial using a quick-reading cloacal thermometer), snout-vent length (measured by stretching snake along measuring tape), sex (determined by probing), stage of ecdysis (post-molt, inter-molt, or pre-molt determined by visual inspection), presence or absence of a food bolus (determined by palpation), presence or absence of evidence of previous injury (visual inspection), and

reproductive status of females (palpation). Ventral scales of all snakes were clipped for future identification should they be recaptured to prevent running multiple trials on any individual. Snakes were then returned unharmed to their site of capture and released.

The video data yielded a total of 19.2 hours of footage. I evaluated and scored the behavior of each snake from videotape in detail (frame by frame). Videotapes were viewed using a Sony EV-A50 8-mm video recorder and a 19-inch television monitor. I initially used an open-ended catalogue to record body postures, antipredator displays, and actions (Table 2), noting the position of the snake's head, anterior body (from head to center of mass), posterior body (from center of mass to vent), and tail during a trial (Arnold & Bennett 1984). Head, body, and tail positions were scored relative to their relative positions and orientations to the predator and to each other. I scored behavior beginning at the predator-exposed threat level and ending upon termination of the post-capture predator-touch threat level. Behavior at distinct stages of the trial were not separately analyzed. This resulted in two minutes of scored behavior for each snake. A posture, display, or action was scored as the number of seconds it occurred in the two-minute period. After all

video data were collected, I transformed these values into the proportion of time a snake exhibited these postures, displays, and actions during a trial. Extremely rare behavior was omitted prior to data analysis. Behavior was defined as rare if it was exhibited by fewer than three individual snakes (regardless of species) out of all 329 snakes, or if it occurred less than an average of 1% of the time in all trials.

Phylogenetic Hypothesis

My ability to identify the phylogenetic components of antipredator behavior hinged upon reference to a "good" phylogenetic hypothesis. Among snakes, the phylogenetic relationships among the Colubridae are poorly understood and no published phylogeny currently exists that includes all species of snakes of my study. However, all of these species have been studied in various phylogenetic contexts and several generally accepted putative monophyletic clades using morphological, and molecular data have been identified (Cope, 1893, 1894; Romer, 1956; Dowling, 1959; Underwood, 1967; Smith et al., 1977; Dowling and Duellman, 1978; Dowling et al., 1983; Cadle, 1984; Dessauer et al. 1987; Densmore et al., 1992; De Queiroz and Lawson, 1994; Knight and Mindell, 1994; Heise et al., 1995; López and Maxson, 1995; Buckley et al. 2000). I constructed an

hypothetical phylogeny with equal branch lengths by assigning my species to their monophyletic clades and then placing those groups according to the best supported relationships with each other (Figure 1). The result was a conservative phylogenetic hypothesis. Snake membership to these monophyletic groups was coded as dummy variables for use as covariables in CCA II to remove the effects of common ancestry (phylogeny) in the variation of antipredator behavior. The phylogenetic groups (and covariable categories) were: 1) *Xenodontinae* (includes the genera *Carphophis*, *Diadophis*, *Heterodon*, *Hypsiglena*, *Sonora*, and *Tantilla*), 2) *Natricinae* (includes the genera *Nerodia*, *Regina*, *Storeria*, *Thamnophis*, and *Virginia*), 3) *Opheodrys*, 4) racers (includes the genera *Coluber* and *Masticophis*), 5) ratsnakes (includes the genera *Pituophis* and *Elaphe*), and 6) kingsnakes (includes the genera *Lampropeltis* and *Rhinocheilus*).

Analytical methodology

Over the past few years, many researchers have returned to the idea that comparisons of species as independent evolutionary units invite Type I statistical errors. Consequently, several methods are being developed to statistically address comparative questions by referencing to or controlling for the constraints of

phylogeny (see reviews in Huey, 1987; Pagel and Harvey, 1988; Gittleman, 1989; Burghardt and Gittleman, 1990; Funk and Brooks, 1990; Gittleman and Kot, 1990; Brooks and McLennan, 1991; Harvey and Purvis, 1991; Miles and Dunham, 1992; Losos and Miles, 1994; Martins and Hansen, 1997).

Miles and Dunham (1992: 848) stated "Because life history traits are likely to be correlated with a species' phylogenetic history, unequivocal evidence for adaptation to local environmental conditions may be recognized only after the variation in a trait attributable to phylogeny is removed." This applies as well to antipredator behavior in snakes. Thus, in order to deduce the ultimate and proximate factors that influence antipredator behavior in snakes, observations must be viewed alternately both within and outside of the constraints of phylogeny.

I used canonical correspondence analysis (CCA) to gauge the phylogenetic components of antipredator behavior in snakes and test for relationships with ultimate and proximate factors after subtracting the variation due to phylogeny. Use of CCA in this context has recently been advanced (Fox and Shipman, in press).

Canonical correspondence analysis is a direct-gradient ordination technique commonly used in community ecology (ter Braak 1988; Palmer 1993; ter Braak and Šmilauer,

1998). It is used to study the occurrence of species found at sampled sites responding in order to environmental gradients that are input as independent continuous or categorical variables. The scores from CCA can be plotted to infer how sites with similar species composition relate to the measured environmental variables and can be easily interpreted graphically by overlaying the scores of sites (plotted as points), species (plotted as points), and environmental variables (plotted as vectors). Sites with similar species composition are grouped together and placed in order along the environmental gradients that best explain or correlate with the observed patterns. Essentially, CCA can be thought of as a special case of multiple regression.

In using CCA for studying antipredator behavior in colubrids, I redefined the variables: individual snakes are "sites" or sample plots, postures, displays, and actions are "species" or dependent variables, and the ultimate and proximate factors are the "environmental" or independent variables. In such an analysis, individual snakes with similar postures, displays, and actions will be ordinated relative to the ultimate and proximate independent variables.

I conducted two primary CCA tests. The first (CCA I) was designed to identify phylogenetic patterns of antipredator behavior and compare these patterns to the relative influences of other ultimate factors (species-specific body size and sex). The influences of proximate factors (body temperature, reproductive condition, evidence of injury, and presence of a food bolus) on antipredator behavior were removed in this CCA by using them as covariables. This partial ordination factors out the amount of variation in the observed antipredator behavior that is due to the estimated influence of these proximate factors, leaving the rest of the variation to be explained by the ultimate factors. Partial ordination is analogous to a partial correlation in multiple regression. To identify phylogenetic patterns, behavior patterns best associated with each species in the CCA were mapped onto a phylogeny (see Phylogenetic Hypothesis above) and Farris character optimization was employed to estimate ancestral and derived behavioral traits (Brooks and McLennan, 1991).

The second CCA (CCA II) removed the variation in antipredator behavior attributable to phylogeny and was used to examine the relative importance of the remaining ultimate factors plus the proximate factors in explaining antipredator behavior. Partial correlation is an accepted

phylogenetic-subtraction method (Pagel and Harvey, 1988). Here, phylogenetic subtraction was accomplished by using membership in monophyletic clades identified a priori as categorical variables and then using them as covariables in partial ordination. This factored out the variation in antipredator behavior resulting from the pattern of common ancestry, leaving the rest of the variation to be explained by the remaining factors. With the exception of the species category variable, the other ultimate factors were retained in this analysis since their influences on antipredator behavior are to some unknown degree correlated with phylogenetic history. In other words, the relationships of these ultimate factors with particular antipredator behavior may be obscured by the overriding influence of phylogenetic effects and might not be apparent unless those phylogenetic effects are first removed. For example, body size (snout-vent length), now becomes a proximate factor as the ontogenetic stage of growth, since the inter-generic differences in adult body size are factored out as a covariable.

To perform these analyses, I used the statistical software package CANOCO 4.0 for Windows (ter Braak and Smilauer, 1998). CANOCO 4.0 performs Monte Carlo permutation tests to evaluate the significance of

relationships between dependent and the independent variables at two levels. The first tests the overall significance of the relationship between the dependent variables and the sum of all canonical axes, with the null hypothesis being no significant relationship between antipredator behavior (dependent variables) and independent variables combined. The second tests whether each ordination axis based on independent variables shows a significant relationship with the dependent variables. In my case, the null hypothesis was no relationship between antipredator behavior and the CCA axis under consideration. Because I conducted two separate CCAs, one to identify phylogenetic components and relative influence of ultimate factors, and the other to compare effects of proximate and ultimate factors (after removing effects of phylogeny) on antipredator behavior, I employed the Bonferoni adjusted p-value ($0.05/2$) as the critical value to reject the null hypothesis for either test.

RESULTS

Phylogenetic relationships of antipredator behavior

For CCA I, there were significant relationships among behavior patterns and the sum of all axes (Monte Carlo test with 9999 permutations, $F = 3.17$, $p = 0.0001$) and there

were significant relationships between individual axes 1-3 the observed patterns of behavior (Table 3).

The scores of snakes on the first three axes of CCA I demonstrate that colubrids exhibited general phylogenetically correlated patterns of antipredator behavior, with overlap among species within phylogenetic groups (Figures 2-3).

Axis one explained the greatest amount of variation in behavior, with axes two and three explaining sequentially less variation as indicated by their eigenvalues, which are a measure of the relative strength and importance of an ordination axis and the amount of variation explained by the axis (Table 3). The overall relationships between the independent variables and specific patterns of behavior are found by examining the position of the plotted behavior patterns with respect to the independent variables. Behavior patterns plotting far beyond the independent-variable vectors and isolated from the other behavior patterns represent relatively rare behavior and should not be used for inference of overall trends, but may be informative for describing apomorphic behavior for individual species. Behavior patterns located close to the origin of the axes are ubiquitous and also less informative for describing overall patterns. Therefore, the

interpretation of the overall pattern is taken from the behavior patterns most closely associated with the terminus of the vectors of independent variables.

As an ultimate independent variable, interspecific body size appears to be the best determinant of antipredator behavior (Figures 4-5). Next, phylogenetic affiliation appears to be important in predicting antipredator behavior in colubrids as indicated by the generally similar directions of the vectors for species within each of the six clades (Figures 4-5).

The first axis (Table 4, Figure 4) shows that behavior diverged primarily on the basis of body size. On axis one, snakes with high negative scores (far left) were xenodontine and other small snake species that exhibited more escape attempts, more open body postures, more exposed and depressed heads not facing the predator but positioned proximally to the predator, and more depressed anterior bodies. Snakes with high positive scores (far right) were mostly large racer and kingsnake species, which were more stationary, had more coiled body postures, tails more centered on their bodies, and more protected and hidden heads centered on their bodies. Natricine species appeared intermediate in these behavior patterns along axis one.

Along axis two (Table 4, Figure 4), variation in behavior was determined primarily by large and medium-sized natricine, racer, and kingsnake species, with negative scores representing behavior patterns having elevated heads facing the predator but not positioned proximal to the predator, with more elevated anterior bodies, and exhibiting more open-mouth strikes. Snakes with high positive scores along axis two were opposed to these behaviors (Table 4). While sex differences appeared to correlate also with axis two, a post-hoc test conducted by reanalysis using snout-vent length as a covariable showed that this was due to sexual dimorphism in body size and not sex-specific differences since the male and female vectors disappeared.

Axis three (Table 4, Figure 5) distinguished the behavioral differences of *H. torquata*, *S. semiannulata*, and *T. gracilis* having more straight body postures and depressed heads vs all other species.

I was able to map major modes of antipredator behavior for head orientation, head position, head exposure, head elevation, anterior body elevation, overall body posture, tail position, escape behavior, striking behavior, tail vibration, and body and tail rubbing behavior. (Figures 6-16). I was not able to map several behavioral characters

because they were either too ubiquitous across all species or were too apomorphic to be phylogenetically informative. The most ubiquitous and hence, plesiomorphic character, was tail exposure. Apomorphic characters were the derived body throwing and tail hiding behavior of *H. torquata*, *R. lecontei*, and *L. getula*, the elevated tail coiling and wriggling of *T. marcianus*, and the ventral exposure of the head and body by *D. punctatus* (in death feigning behavior).

Proximate and ultimate causes of antipredator behavior

The second CCA tested for the relationships of ultimate and proximate factors with expressed antipredator behavior after removing the effects of phylogeny. Overall relationships of all axes with behavior were significant (Monte Carlo test with 9999 permutations, $F = 1.73$, $p = 0.0002$).

The relationship of behavior patterns specifically with axes one and two were significant (Table 5). After removing the effects of phylogeny, body condition factors, sex, body temperature, reproductive status (gravid vs non-gravid) and ontogenetic growth stage (as indicated by snout-vent length) were important determinants of antipredator behavior in colubrids (Figure 17).

On axis one (Table 6; Figure 17), gravid snakes, snakes with a food bolus, snakes with evidence of previous

injury, snakes in pre-molt stage, and male snakes attempted to escape more, had more open body postures, exhibited more open-mouth strikes, had their tails positioned lateral to the predator, and had their heads oriented facing or lateral to the predator. Female snakes in postmolt or intermolt stage escaped directionally away from the predator, had elevated tails positioned centered on their bodies or proximal to the predator, and presented more tail coiling, tail rubbing, and tail wriggling behavior, hid their heads more, oriented their heads away from the predator, and positioned their heads distally from the predator.

Along axis two (Table 6; Figure 17), larger snakes and cooler snakes exhibited more body rubbing behavior, more open-mouth strikes, more tail vibration, more coiled body postures, positioned their tails more lateral to the predator, and had more elevated and protected heads compared with smaller and warmer snakes.

DISCUSSION

The observed phylogenetic pattern of response of snakes in CCA I underscores the importance of incorporating phylogeny into a study of antipredator behavior of these snakes and confirms the utility of my methods to interpret

patterns among species. Prior to any discussion, however, it is important to review the constraints and framework of my study design.

While the standardized predator effigy elicited predictable and repeatable responses in snakes, it was not a real predator that is encountered by these snakes in their natural environment and the significance with respect to a real medium to large-sized canid predator can only be approximated. Although observed antipredator behavior by the snakes seemed to be directed toward the predator effigy in every case, I was in partial view of snakes during the trials with unknown influence. Still, it would not be feasible to conduct a comparative study using real predators in an experimental fashion, and it is unlikely that enough observations of predator encounters could be observed in the field since such observations are extremely rare (Jackson et al., 1976). Moreover, there appears to be consensus among researchers of antipredator behavior in snakes that repeatable responses are observed regardless of the physical make-up of predator models used (Shine et al., 2000). In future studies, it would be easy to experimentally manipulate cues of predator models and look for differences in responses. Also, habitat context, a factor that has been shown to influence antipredator

behavior in snakes (Greene, 1979; Golani and Kochva, 1988; Duvall et al., 1985), was artificial (but controlled) in this study. Again, with respect to the overall design, habitat structure in the arena could also be manipulated in future studies. Lastly, I call attention to the fact that all of these snakes rely first on crypsis, the avoidance of detection by predators as an antipredator strategy. In my study, I focused on the post-detection antipredator behavior of snakes, which has been previously studied by examining only simple measures of incidence of biting or escape behavior. Even with these constraints and limitations, however, my data supplied patterns such that broad and general inferences could be made about the evolution of antipredator behavior in snakes and the ultimate and proximate determinants associated with that behavior.

Evolution of antipredator behavior in colubrids

By mapping species-specific behavior patterns onto a phylogeny, I was able to use character optimization to estimate the ancestral states for several antipredator responses in colubrids. These ancestral states are as follows: head facing predator less (figure 6), head less centered on body (figure 7), head more exposed (figure 8), head not elevated (figure 9), anterior body more depressed

(Figure 10), more open, uncoiled overall body posture (Figure 11), tail less centered on body (Figure 12), more escape attempts (Figure 13), less open-mouth strikes (Figure 14), less body/tail rubbing (figure 15), and less tail vibration (figure 16). If the phylogenetic relationship of the major groups of colubrids is roughly correct, the evolution of more active antipredator behavior patterns evolved at least twice in the colubrids studied here - at some point in the divergence of natricines and in the ancestor to racers, ratsnakes, and kingsnakes (Figures 6-16).

Many of the behavioral modes also contained synapomorphies and therefore are potentially useful for making phylogenetic inferences. As such, they should be added to morphological, molecular, and other behavioral data for the development of a more complete and robust phylogenetic hypothesis for these species. In terms of overall similarity of antipredator behavior, the first CCA generally supports the phylogenetic groups used in this study. Exceptions to this were the divergence of *T. marcianus* and *R. grahami* from the other natricine snakes, and *H. torquata* from the other xenodontine species (Figures 4-5). Compared with the majority of natricine species, *T. marcianus* and *R. grahami* exhibited more coiled body

postures, more tail rubbing, more tail coiling, more tail wriggling, positioned their tails more centered on their bodies, and had their heads hidden more and positioned more centered on their bodies. Among xenodontine species, *H. torquata* had more coiled body postures (Figures 4-5). Another observation of note is that *O. aestivus*, while currently considered less basal than the Natricinae, exhibited a repertoire of antipredator behavior that was almost entirely plesiomorphic (Figures 6-16).

While the higher taxonomy of major groups of snakes has recently been advanced (Cadle, 1987, 1988, 1992; Dessauer et al., 1987; McDowell, 1987), the current state of understanding of phylogenetic relationships within colubrid snake systematics is poor and in disarray (López and Maxson, 1995). Note that while the detailed topology of phylogenetic relationships of colubrids in this study does not affect the analyses of ultimate and proximate determinants of snake antipredator behavior, it (exact topology) is obviously very important for inferring the evolution of particular traits. As such, I acknowledge the highly unresolved condition of colubrid snake systematics and understand that the mapping of these traits should be considered a work in progress, to be modified with future knowledge of relationships. Perhaps these data could be

helpful in the pursuit of this objective. The Colubridae are a large and diverse group of snakes, and many taxa have not been represented in this study. It will be fascinating to learn how the evolution of antipredator behavior in this group of snakes becomes better resolved with future studies of phylogenetic relationships.

Ultimate and proximate determinants

The most important ultimate factor was inter-specific body size, as indicated by its long vector along axes one and two in the first CCA. This factor was significantly correlated with major patterns of antipredator behavior. Larger species generally exhibited more protected and elevated heads facing positioned more centered on their bodies, vibrated their tails more, had more coiled body postures, more elevated anterior bodies, had more body rubbing, were more stationary, and presented more open-mouth strikes. The ancestral colubrid was most likely a small fossorial snake with simple antipredator behavior similar to most of the xenodontine snakes in this study, which were more plesiomorphic in their antipredator behavior.

The small-bodied xenodontine snakes in this study were mostly fossorial species. For the most part they exhibited very simple antipredator behavior patterns (except for *D.*

punctatus, which exhibited death feigning) of escaping and attempting to escape by cover (Figure 4), since biting most likely would be ineffective against a predator. Although these species possess rear fangs and Duvernoy's gland secretions, the aperture of their mouths and effectiveness of the use of any "venom" is constrained by their small body size. The larger and more terrestrial members of this group, *H. platyrhinos* and *H. torquata*, have divergent antipredator behavior. Increased body size and use of more terrestrial and aquatic habits are coevolved traits, probably due to the functional constraint upon body size in more fossorial snakes.

Body size was also an important determinant of antipredator behavior in CCA II as a proximate factor of ontogenetic growth stage. Larger snakes exhibited generally more active antipredator behavior patterns. This contrasts with pitvipers (Chapter 1), in which larger snakes exhibited more passive defense patterns. This may reflect the role of venom as the primary organizer of antipredator behavior in venomous species. Also in support of this idea, pitvipers exhibited more derived and species-specific antipredator behavior than the colubrids, with intra-specific variation being less than inter-specific variation. As mentioned previously, the xenodontine

species in this study are rear fanged and have a type of venom (Duvernoy's gland secretions). The use of venom by these species was not employed in active defense in my study and these species rarely struck at the predator. Thus, it does not appear that Duvernoy's secretions played an overt role in molding the evolution of antipredator behavior in these xenodontine species. Not yet thoroughly studied are the elapids, the sister clade (López and Maxson, 1995) to colubrids. Study of elapid species would be useful in determining the influence of venom in shaping the evolution of antipredator behavior in snakes.

An unexpected result was the more stationary behavior mode found in the racer clade. These snakes, as their common descriptor implies, are noted for their reliance on speedy escape from predators. This lack of flight was most likely due to the simple, controlled environment of the arena in which trials took place; there were no obvious escape routes. It would be useful to study the effects of habitat and escape route availability to better understand these observations.

My results, like previous studies, showed an inverse relationship between striking behavior and body temperature. Studies of the relationship between body temperature and antipredator behavior in snakes (mostly

garter snakes, *Thamnophis spp.*) are contradictory to each other. The majority of work indicates that colder snakes are more likely to use more active antipredator defense (Fitch, 1965; Heckrotte, 1967; Arnold and Bennett, 1984; Costanzo, 1986; Passek and Gillingham, 1997; Shine et al., 2000). Schieffelin and de Quieroz (1991) and Keogh and Deserto (1994) found the opposite. My research corroborates the results of the majority of past studies as warmer snakes in my study had a more passive antipredator behavioral complex in that they were less apt to strike, vibrated their tails less, exhibited more depressed and open (less coiled) body postures, had their heads more depressed, oriented away from the predator, and positioned distally from the predator, and escaped more away from or toward the predator. Since warmer body temperatures afford snakes better capacity for locomotor performance (Siegel et al., 1987), they may have no need for active displays and defense because they can rely more on escape than confrontation.

Body condition factors such as pre-molt stage of ecdysis, evidence of previous injury, presence of a food bolus, and gravid reproductive stage associated with more active antipredator behavior patterns. Explanation for this may borrow from the same reasoning used for the

effects of cool body temperature, with these factors limiting locomotor and sensory performance. Stress has been shown to have effects on behavior due to increased cortisol levels (Schuett and Grober, 2000). Males were also shown to have more active defense behavior patterns compared with females, I have no direct explanation for this difference other than generally increased male aggression as found in other taxa.

In summary, my integrative approach allowed me to infer both "why" and "how" colubrids exhibit specific antipredator behavior. Both ultimate and proximate factors have shaped the expression of antipredator behavior.

At the ultimate level of causation, I determined that colubrid snakes showed generally phylogenetically identifiable modes of antipredator defense. More phylogenetically basal, fossorial, and small-bodied species of colubrids were overall plesiomorphic in their antipredator behavior, indicating that diverse and more active patterns of antipredator behavior did not evolve until increased body size and use of more aquatic and terrestrial habits evolved.

At the proximate level, larger snakes and snakes with possibly decreased physical performance exhibited more active antipredator behavior. The observation that large-

bodied colubrids had more active antipredator behavior is in opposition to that found in pitvipers (Chapter 1), calling attention to the important role venom plays in shaping antipredator defense in snakes.

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Table 1. Numbers of each species by sex, and snout-vent lengths for snakes used in antipredator trials.

Location	Species	N				SVL		
		Total	Males	Females	Juveniles	Minimum	Maximum	Mean
Arizona								
	<i>Diadophis punctatus</i>	3	1	2	0	307	407	361.3
	<i>Hypsiglena torquata</i>	8	3	4	1	156	330	273.3
	<i>Lampropeltis getula</i>	11	7	4	0	322	843	568.1
	<i>Lampropeltis triangulum</i>	1	0	1	0	320	320	320.0
	<i>Masticophis bilineatus</i>	3	1	2	0	563	1000	821.3
	<i>Pituophis catenifer</i>	11	8	3	0	278	1122	748.2
	<i>Rhinocheilus lecontei</i>	12	3	9	0	392	634	517.7
	<i>Thamnophis marcianus</i>	12	4	7	1	157	595	359.7
Arkansas								
	<i>Carphophis vermis</i>	14	4	9	1	92	250	204.6
	<i>Masticophis flagellum</i>	2	1	1	0	479	1123	801.0
	<i>Coluber constrictor</i>	13	8	5	0	285	985	726.8
	<i>Diadophis punctatus</i>	35	6	28	1	69	280	198.7
	<i>Elaphe emoryi</i>	2	1	1	0	942	1092	1017.0

Table 1 continued

Location	Species	N				SVL		
		Total	Males	Females	Juveniles	Minimum	Maximum	Mean
Arkansas								
	<i>Elaphe obsoleta</i>	13	8	5	0	170	1650	1051.8
	<i>Heterodon platyrhinos</i>	2	1	1	0	474	620	547.0
	<i>Lampropeltis getula</i>	7	4	3	0	270	1150	786.6
	<i>Lampropeltis triangulum</i>	3	1	2	0	205	370	286.7
	<i>Lampropeltis calligaster</i>	3	2	1	0	522	966	791.3
	<i>Nerodia erythrogaster</i>	6	3	3	0	240	835	520.5
	<i>Nerodia sipedon</i>	6	2	4	0	150	746	468.5
	<i>Opheodrys aestivus</i>	7	2	4	1	127	425	284.6
	<i>Storeria dekayi</i>	4	0	4	0	195	236	210.5
	<i>Storeria occipitomaculata</i>	10	0	9	1	143	260	183.5
	<i>Tantilla gracilis</i>	3	1	2	0	153	195	168.7
	<i>Thamnophis sirtalis</i>	11	4	7	0	182	671	446.2
	<i>Virginia valeriae</i>	8	2	6	0	130	240	193.0
Oklahoma								
	<i>Coluber constrictor</i>	18	11	7	0	195	821	526.9
	<i>Masticophis flagellum</i>	1	0	1	0	1203	1203	1203.0

Table 1 continued

Location	Species	N			SVL			
		Total	Males	Females	Juveniles	Minimum	Maximum	Mean
Oklahoma								
	<i>Diadophis punctatus</i>	4	2	2	0	187	296	248.0
	<i>Elaphe emoryi</i>	2	1	1	0	835	928	881.5
	<i>Elaphe obsoleta</i>	11	3	8	0	319	1078	539.5
	<i>Lampropeltis calligaster</i>	5	3	2	0	291	961	662.0
	<i>Nerodia erythrogaster</i>	5	2	3	0	182	956	599.6
	<i>Nerodia rhombifer</i>	7	2	5	0	242	752	432.6
	<i>Opheodrys aestivus</i>	7	2	5	0	143	487	341.9
	<i>Pituophis catenifer</i>	1	1	0	0	1042	1042	1042.0
	<i>Regina grahami</i>	3	1	2	0	440	836	633.7
	<i>Sonora semiannulata</i>	9	2	7	0	167	255	209.8
	<i>Storeria dekayi</i>	9	5	4	0	139	240	171.3
	<i>Thamnophis sirtalis</i>	13	6	7	0	292	686	463.4
	<i>Thamnophis proximus</i>	24	13	11	0	238	743	459.7

Table 2. Catalog of observed antipredator behavior in colubrids.

Head Elevation

- 1 HELEV - Head elevated above substrate
- 2 HDEPR - Head depressed onto substrate

Head Exposure

- 3 HHIDE - Head hidden from view
- 4 HPROT - Head protected
- 5 HEXPO - Head exposed and unprotected
- 7 HVEXP - Head ventral surface exposed

Head Orientation

- 7 HAWAY - Head facing away from predator
- 8 HLATR - Head oriented laterally to predator
- 9 HFACE - Head facing predator

Head Position

- 10 HCENB - Head centered on main mass of body
- 11 HDISB - Head positioned distal to the predator
- 12 HLATB - Head positioned lateral to the predator
- 13 HPROX - Head positioned proximal to the predator

Head Displays/Actions

- 14 MGAPE - Mouth gape
- 15 CSTRI - Closed mouth strike
- 16 OSTRI - Open mouth strike
- 17 LATHD - Lateral head display

Posterior Body Elevation

- 18 BPDEP - Posterior body depressed onto substrate
- 19 BPELE - Posterior body elevated above substrate

Anterior Body Elevation

- 20 BADEP - Anterior body depressed onto substrate
- 21 BAELE - Anterior body elevated above substrate

Table 2 continued...

Posterior Body Exposure

22 BPVEX - Posterior venter exposed

Anterior Body Exposure

23 BAVEX - Anterior venter exposed

Composite Body Postures

24 BASYM - Body in asymmetrical coil

25 BTCOI - Body in a tight coil

26 BLCOI - Body in a loose coil

Anterior Body Postures

27 BACOI - Anterior body coiled

28 BASIN - Anterior body postured sinusoidally

29 BASTR - Anterior body postured straight

Posterior Body Postures

30 BPCOI - Posterior body coiled

31 BPSIN - Posterior body postured sinusoidally

32 BPSTR - Posterior body postured straight

Body Actions

33 AESCA - Escape away from predator

34 LESCA - Escape lateral from predator

35 TESCA - Escape toward predator

36 STATI - Body stationary

37 BTHRO - Erratic body throw

38 COESC - Escape attempt under cover as evident by pressing head into substrate, sides, or corners of arena

39 BDRUB - rubbing the ventral and dorsal surfaces of the body together

Tail Elevation

40 TDEPR - Tail depressed onto substrate

41 TELEV - Tail elevated off substrate

Table 2 continued...

Tail Exposure

- 42 THIDD - Tail covered from view
- 43 TEXPO - Tail exposed to view
- 44 TVENT - Tail venter exposed

Tail Postures

- 45 TPROX - Tail positioned proximal to predator
- 46 TLATR - Tail positioned lateral to head
- 47 TDIST - Tail positioned distal to predator
- 48 TCENT - Tail centered on main mass of body

Tail Actions/Displays

- 49 TLRUB - Tail rubbed over body or head
 - 50 TCOIL - Tail coiled/curled
 - 51 TWRIG - Tail wriggled
 - 52 TVIBR - Tail vibrated
-

Table 3. Eigenvalues, *F*-statistics, and *p*-values for first four axes from CCA I.

Axis	Eigenvalue	<i>F</i>	<i>p</i>
1	0.089	26.93	0.0001
2	0.055	20.98	0.0003
3	0.025	9.75	0.0015
4	0.012	7.49	0.0288

Table 4. Behavior scores for first three axes in CCA I
(positive and negative scores that are explained best by
each axis).

Axis One			Axis Two			Axis Three		
Pos. Scores	Neg. Scores		Pos. Scores	Neg. Scores		Pos. Scores	Neg. Scores	
BTCOI	2.27	HVEXP -1.85	TVENT	2.68	OSTRI -1.31	BTHRO	3.17	MGAPE -1.34
TCENT	1.80	BPVEX -1.28	TCOIL	2.55	BAELE -1.09	THIDD	2.34	
TLRUB	1.45	BAVEX -1.27	TELEV	2.25	HELEV -0.71	BPSTR	1.29	
TVIBR	1.45	TESCA -1.02	TWRIG	1.84	HFACE -0.57	BASTR	0.96	
BPCOI	1.41	TDIST -0.52	COESC	1.82	HPROT -0.43	HDEPR	0.51	
HCENB	1.39	HEXPO -0.49	BADEP	0.26	TDEPR -0.18	HDISB	0.31	
HHIDE	1.36	BASIN -0.45				HAWAY	0.27	
BACOI	1.29	BPSIN -0.45				HLATE	0.23	
BDRUB	1.23	HPROB -0.44				LESCA	0.15	
BLCOI	1.06	AESCA -0.32						
STATI	0.29	TPROX -0.19						
BBALL	0.27	HLATB -0.15						
		TLATR -0.14						
		TEXPO -0.11						
		BPDEP -0.04						

Table 5. Eigenvalues, F -statistics,
and p -values for first three axes
from CCA II.

Axis	Eigenvalue	F	p
1	0.019	6.15	0.0013
2	0.011	4.60	0.0088
3	0.006	3.62	0.0624

Table 6. Behavior scores for first two axes in CCA II (positive and negative scores that are explained best by each axis).

Axis One				Axis Two			
Pos. Scores		Neg. Scores		Pos. Scores		Neg. Scores	
HVEXP	2.37	COESC	-1.10	MGAPE	2.13	TLRUB	-1.25
BPVEX	1.88	LESCA	-0.58	BDRUB	1.08	TESCA	-0.75
BAVEX	1.81	HLATB	-0.48	TVIBR	0.86	TDIST	-0.60
BTHRO	1.61	TLATR	-0.40	BLCOI	0.85	HPROB	-0.34
BPSTR	1.55	HEXPO	-0.30	OSTRI	0.84	HDEPR	-0.28
BASTR	1.48	BPSIN	-0.25	BPCOI	0.69	BADEP	-0.21
BBALL	1.15	BASIN	-0.23	BAELE	0.66		
TELEV	0.97	HFACE	-0.20	BACOI	0.64		
TWRIG	0.78	HLATE	-0.20	HCENB	0.53		
TCOIL	0.77	TDEPR	-0.09	HPROT	0.50		
BTCOI	0.75	TEXPO	-0.07	HELEV	0.27		
TVENT	0.73	BPDEP	-0.04				
THIDD	0.73						
AESCA	0.60						
HDISB	0.48						
HAWAY	0.48						
TCENT	0.41						
HHIDE	0.35						
TPROX	0.34						
STATI	0.17						

FIGURE LEGENDS

Figure 1. Phylogenetic hypothesis of colubrids in this study from Cope (1893, 1894), Romer (1956), Dowling (1959), Underwood (1967), Smith et al. (1977), Dowling and Duellman (1978), Dowling et al. (1983), Cadle (1984), Dessauer et al. (1987), Densmore et al. (1992), De Queiroz and Lawson (1994), Knight and Mendel (1994), Heise et al. (1995), López and Maxson (1995), Buckley et al. (2000). Groups were: 1) Xenodontinae, 2) Natricinae, 3) Ophedrys, 4) racers, 5) ratsnakes, and 6) kingsnakes.

Figure 2. Snake scores by phylogenetic group for axes 1 & 2 in CCA I.

Figure 3. Snake scores by phylogenetic group for axes 1 & 3 in CCA I.

Figure 4. Behavior scores and vectors of ultimate independent variables (M = male, F = female, and SVL) for axes 1 & 2 in CCA I. CAVE = *Carphophis vermis*, COCO = *Coluber constrictor*, DIPU = *Diadophis punctatus*, ELOB = *Elaphe obsoleta*, ELEM = *Elaphe emoryi*, HEPL = *Heterodon platyrhinos*, HYTO = *Hypsiglena torquata*, LACA = *Lampropeltis calligaster*, LAGE = *Lampropeltis getula*, LATR

= *Lampropeltis triangulum*, MABI = *Masticophis bilineatus*,
 MAFL = *Masticophis flagellum*, NEER = *Nerodia erythrogaster*,
 NESI = *Nerodia sipedon*, NERH = *Nerodia rhombifer*, OPAE =
Opheodrys aestivus, PICA = *Pituophis catenifer*, REGR =
Regina grahami, RHLE = *Rhinocheilus lecontei*, SOSE = *Sonora*
semiannulata, STDE = *Storeria dekayi*, STOC = *Storeria*
occipitomaculata, TAGR = *Tantilla gracilis*, THMA =
Thamnophis marcianus, THPR = *Thamnophis proximus*, THSI =
Thamnophis sirtalis, VIVA = *Virginia valeriae*. Refer to
 Table 2 for behavior codes.

Figure 5. Behavior scores and vectors of ultimate
 independent variables (M = male, F = female, and SVL) for
 axes 1 & 3 in CCA I. CAVE = *Carphophis vermis*, COCO =
Coluber constrictor, DIPU = *Diadophis punctatus*, ELOB =
Elaphe obsoleta, ELEM = *Elaphe emoryi*, HEPL = *Heterodon*
platyrhinos, HYPO = *Hypsiglena torquata*, LACA =
Lampropeltis calligaster, LAGE = *Lampropeltis getula*, LATR
 = *Lampropeltis triangulum*, MAFL = *Masticophis flagellum*,
 NEER = *Nerodia erythrogaster*, NESI = *Nerodia sipedon*, NERH
 = *Nerodia rhombifer*, OPAE = *Opheodrys aestivus*, PICA =
Pituophis catenifer, REGR = *Regina grahami*, RHLE =
Rhinocheilus lecontei, SOSE = *Sonora semiannulata*, STDE =
Storeria dekayi, STOC = *Storeria occipitomaculata*, TAGR =

Tantilla gracilis, THMA = *Thamnophis marcianus*, THPR = *Thamnophis proximus*, THSI = *Thamnophis sirtalis*, VIVA = *Virginia valeriae*. *Masticophis bilineatus* (MABI) is not shown here due to its short vector along both axes. Refer to Table 2 for behavior codes.

Figure 6. Evolution of head orientation in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 7. Evolution of head position in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 8. Evolution of head exposure in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 9. Evolution of head elevation in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 10. Evolution of anterior body elevation in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 11. Evolution of overall body posture in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 12. Evolution of tail position in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 13. Evolution of escape behavior in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 14. Evolution of open-mouth strike behavior in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 15. Evolution of body and tail rubbing behavior in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 16. Evolution of tail vibration in colubrids. States are as observed for species and estimated by character optimization for ancestral states (Brooks and McLennan, 1991).

Figure 17. Behavior scores and vectors of proximate independent variables (FEMALE, MALE, SVL, GRAVID, POSTMOLT = post-molt stage of ecdysis, INTMOLT = intermolt stage of ecdysis, PREMOLT = premolt stage of ecdysis, BT = body temperature, BOL = presence of a food bolus, and INJ = evidence of previous injury) for axes 1 & 2 in CCA II. Refer to Table 2 for behavior codes.

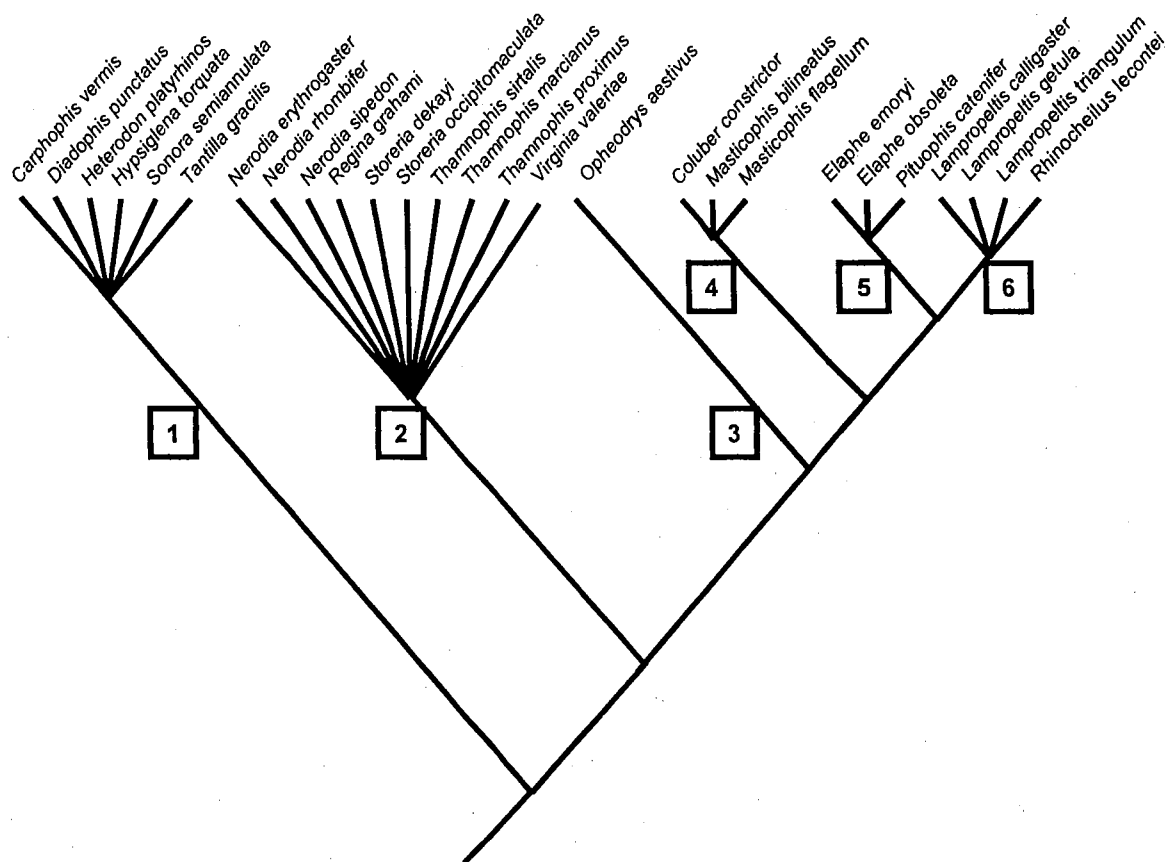


Figure 1

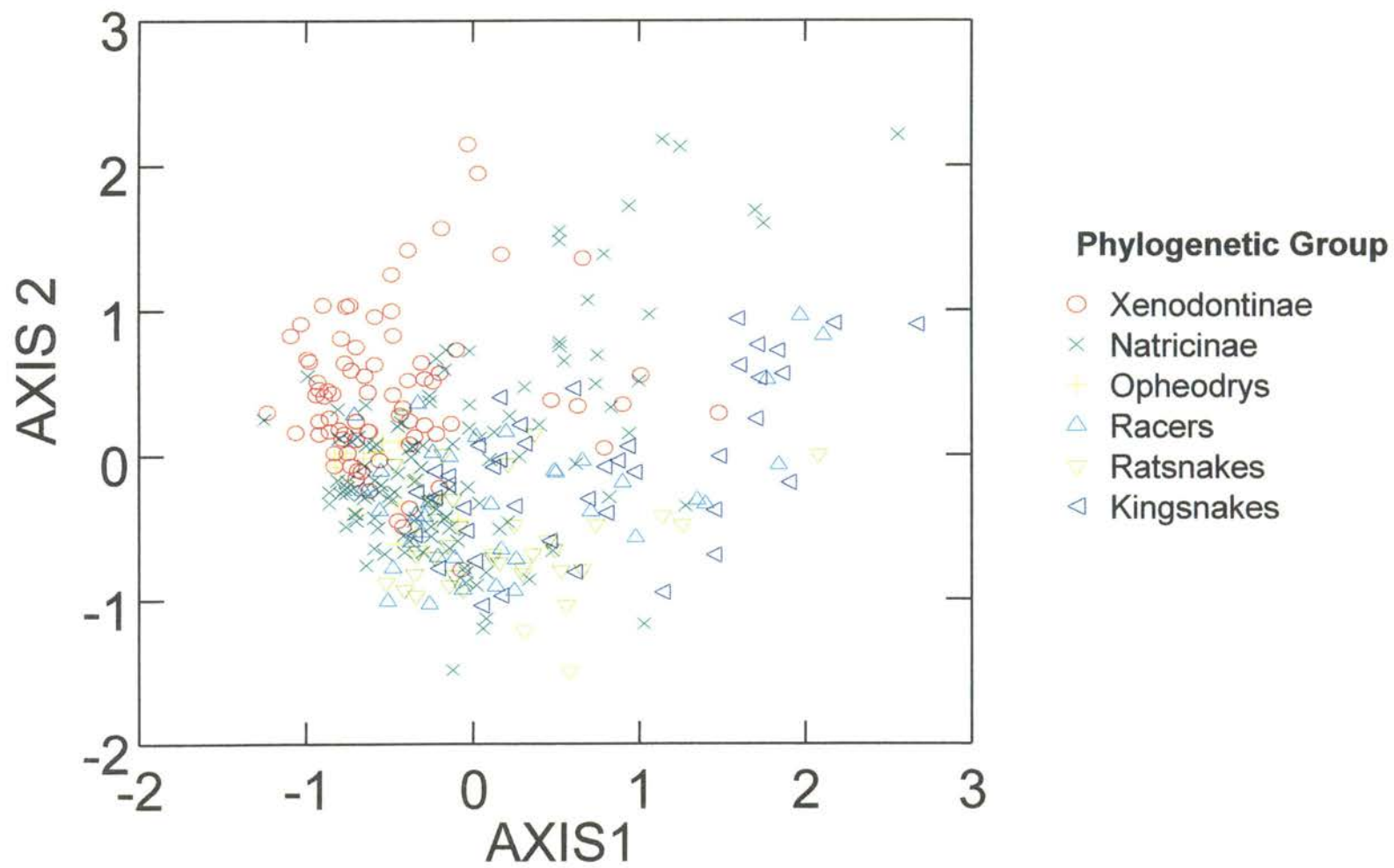


Figure 2

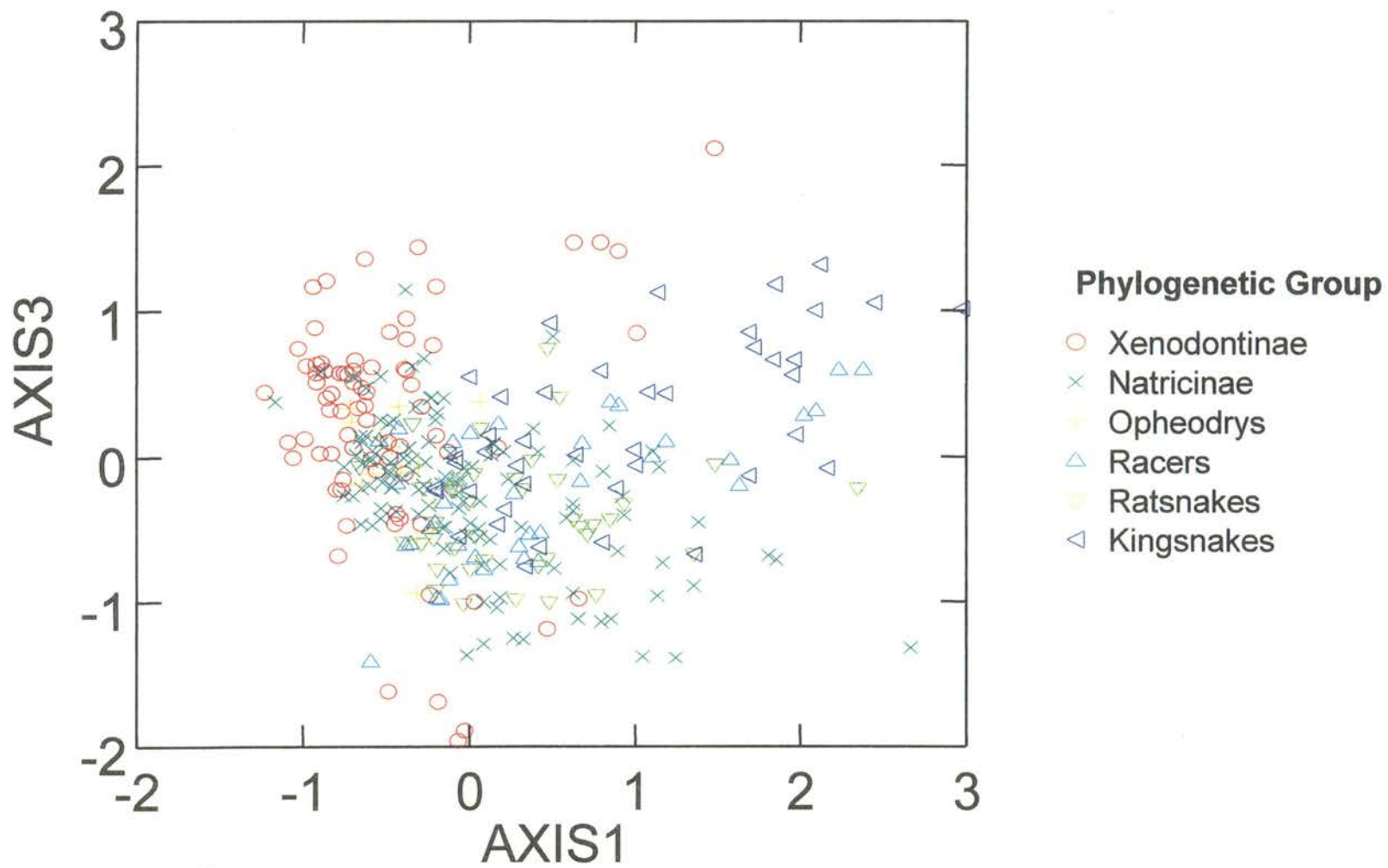


Figure 3

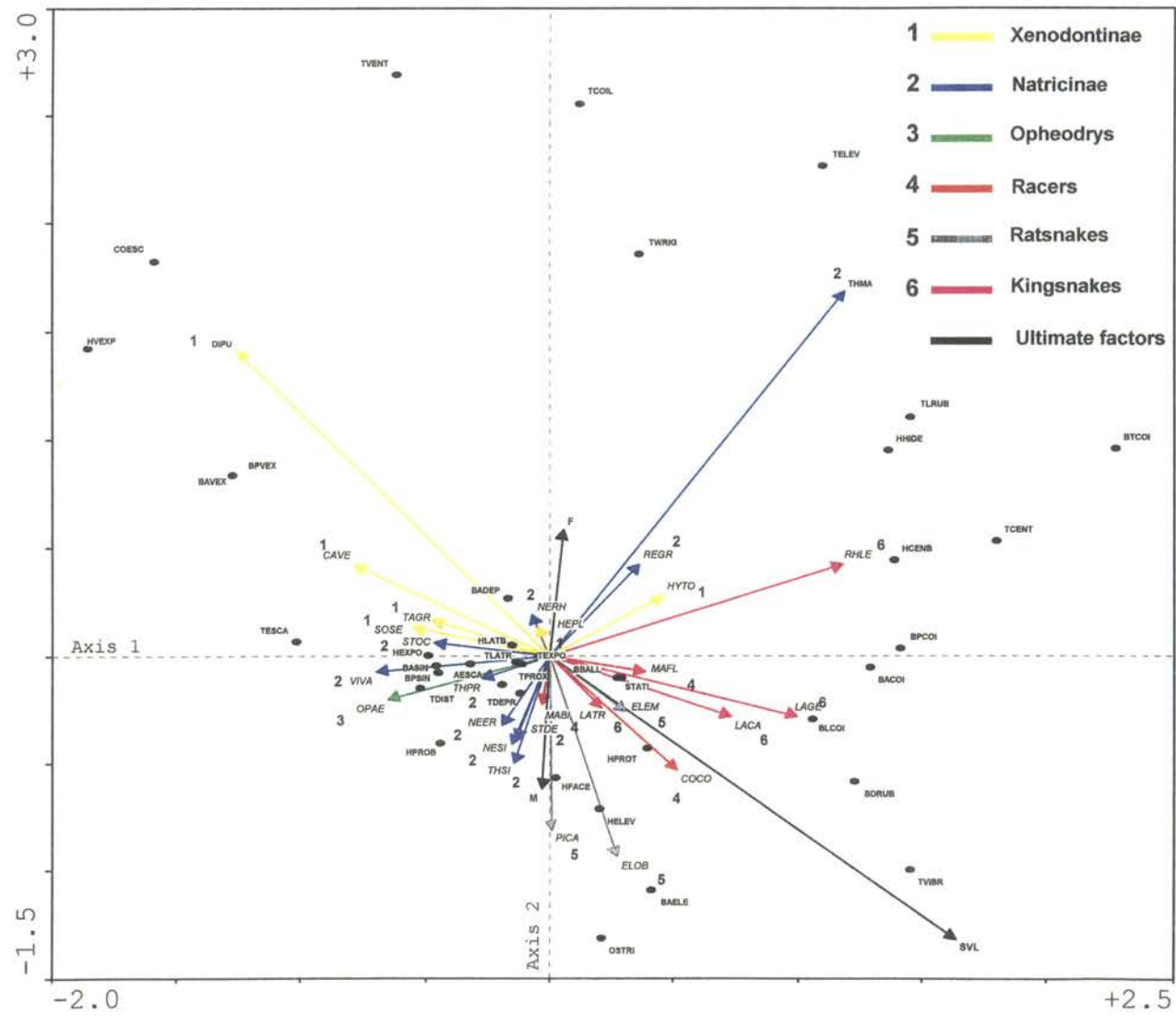


Figure 4

HEAD ORIENTATION

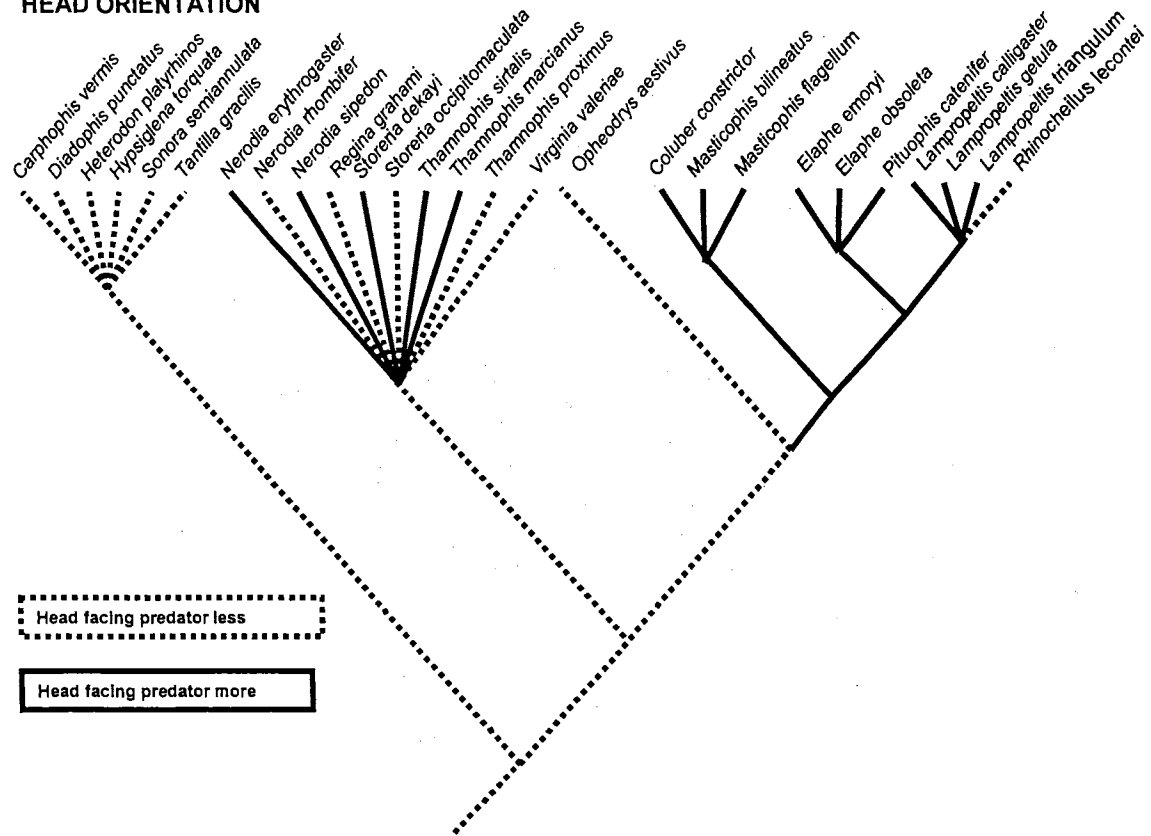


Figure 6

HEAD POSITION

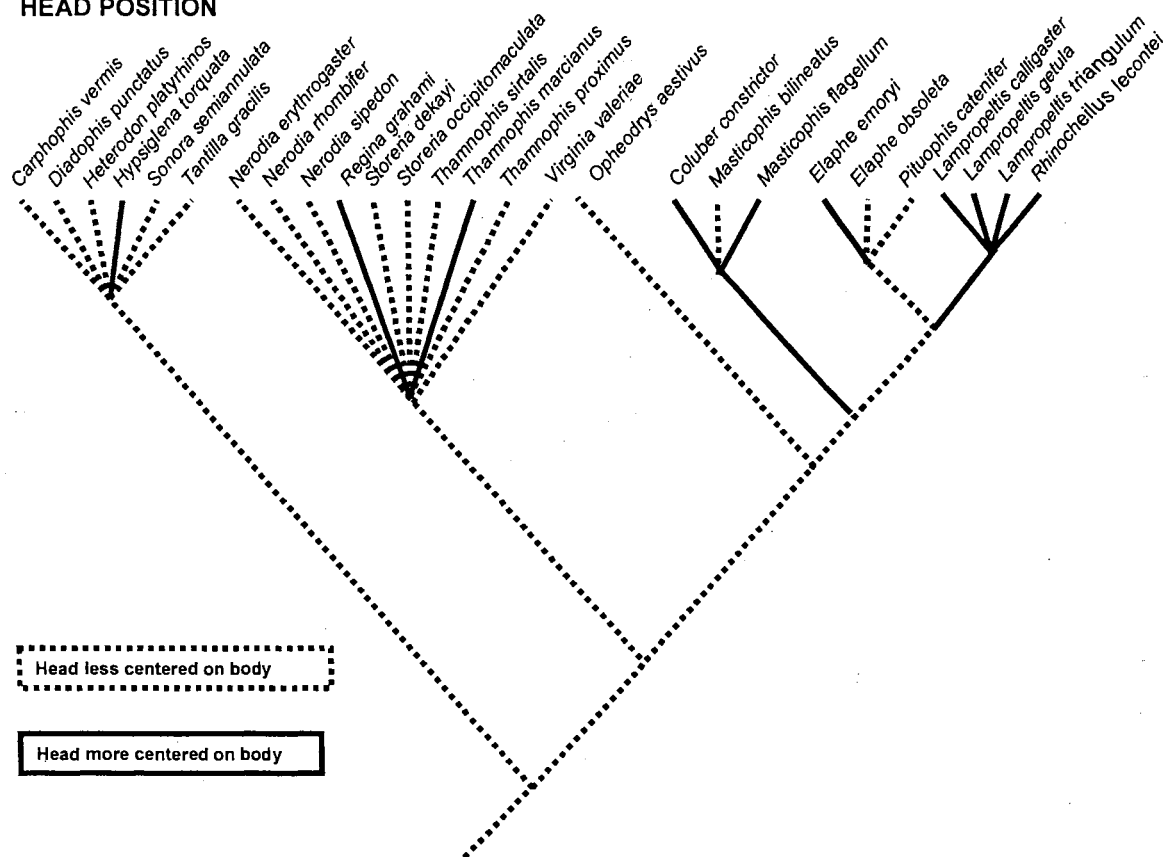


Figure 7

HEAD EXPOSURE

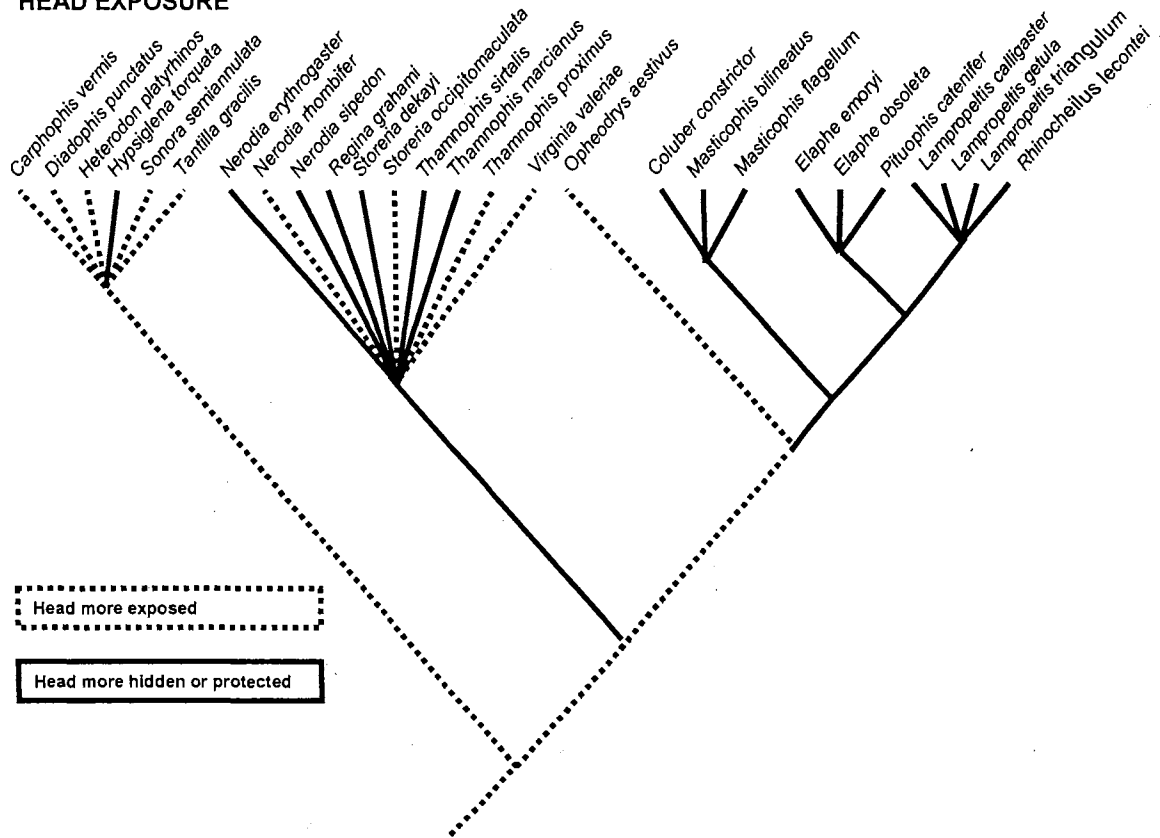


Figure 8

HEAD ELEVATION

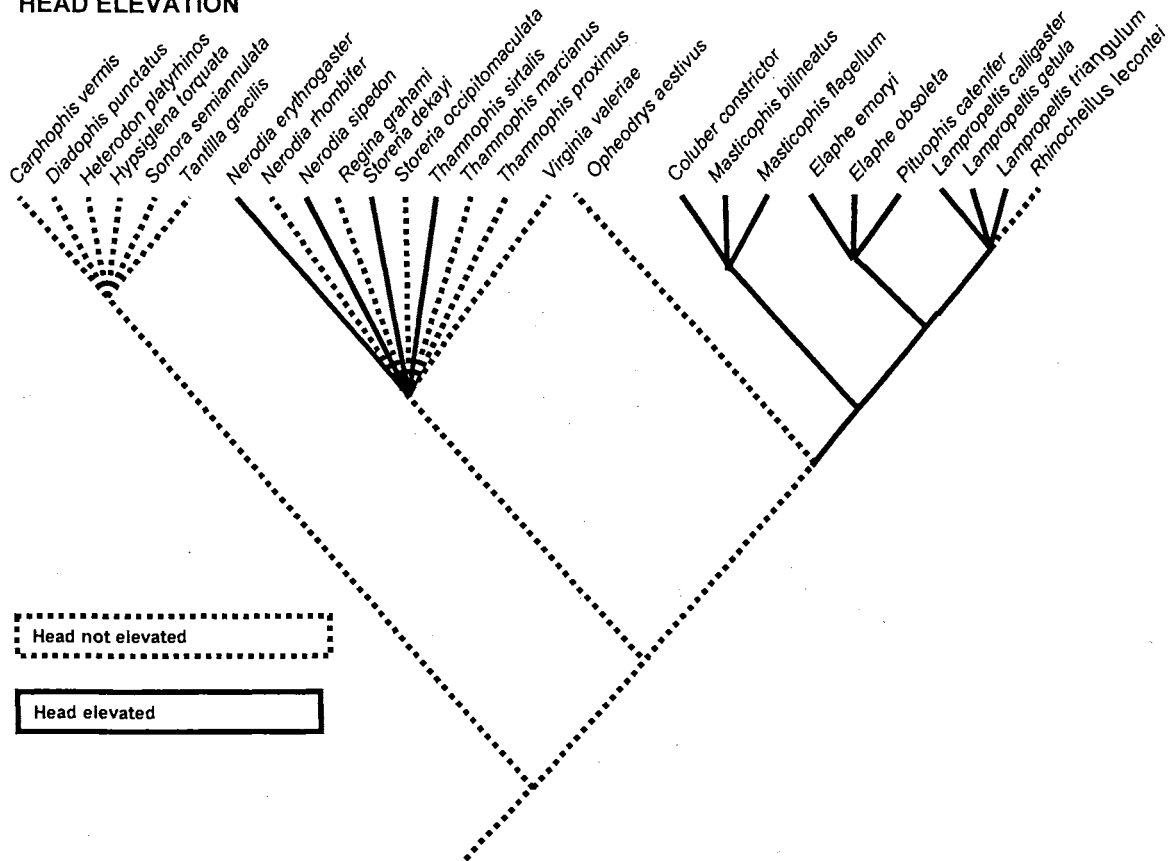


Figure 9

ANTERIOR BODY ELEVATION

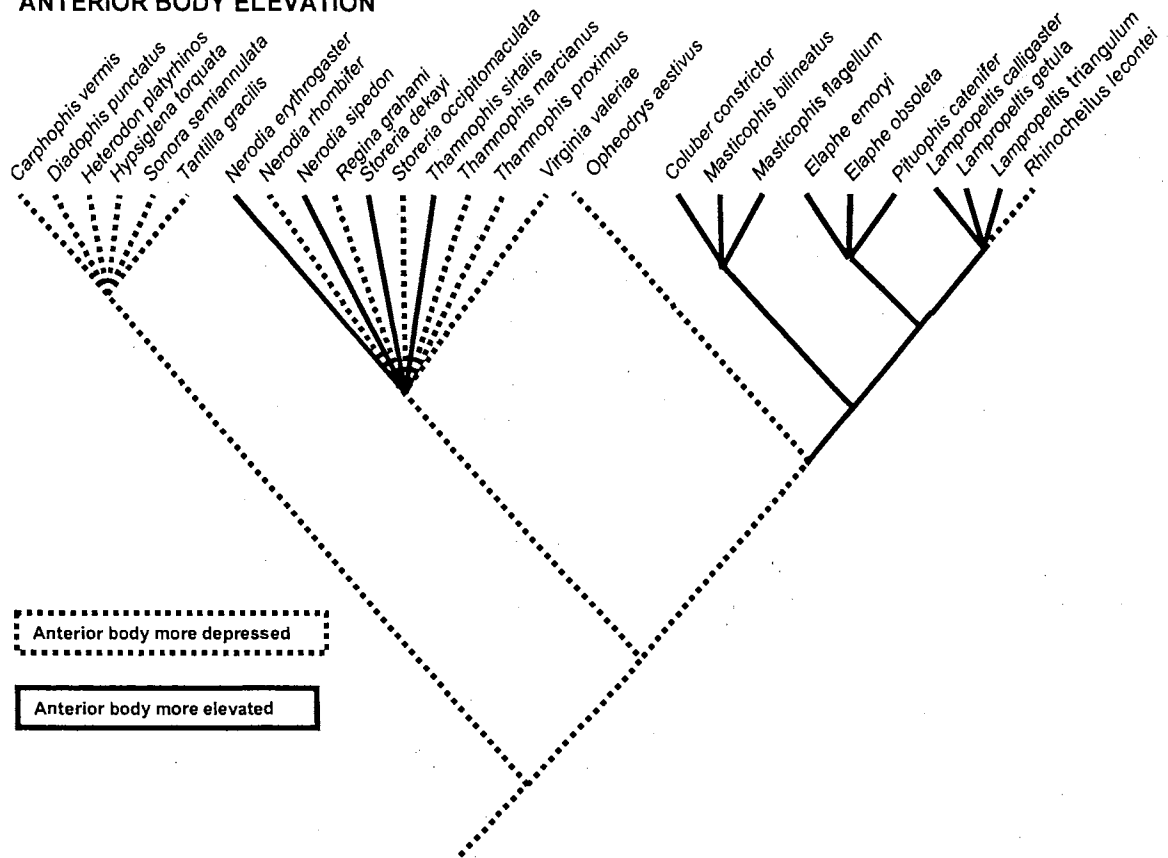


Figure 10

OVERALL BODY POSTURE

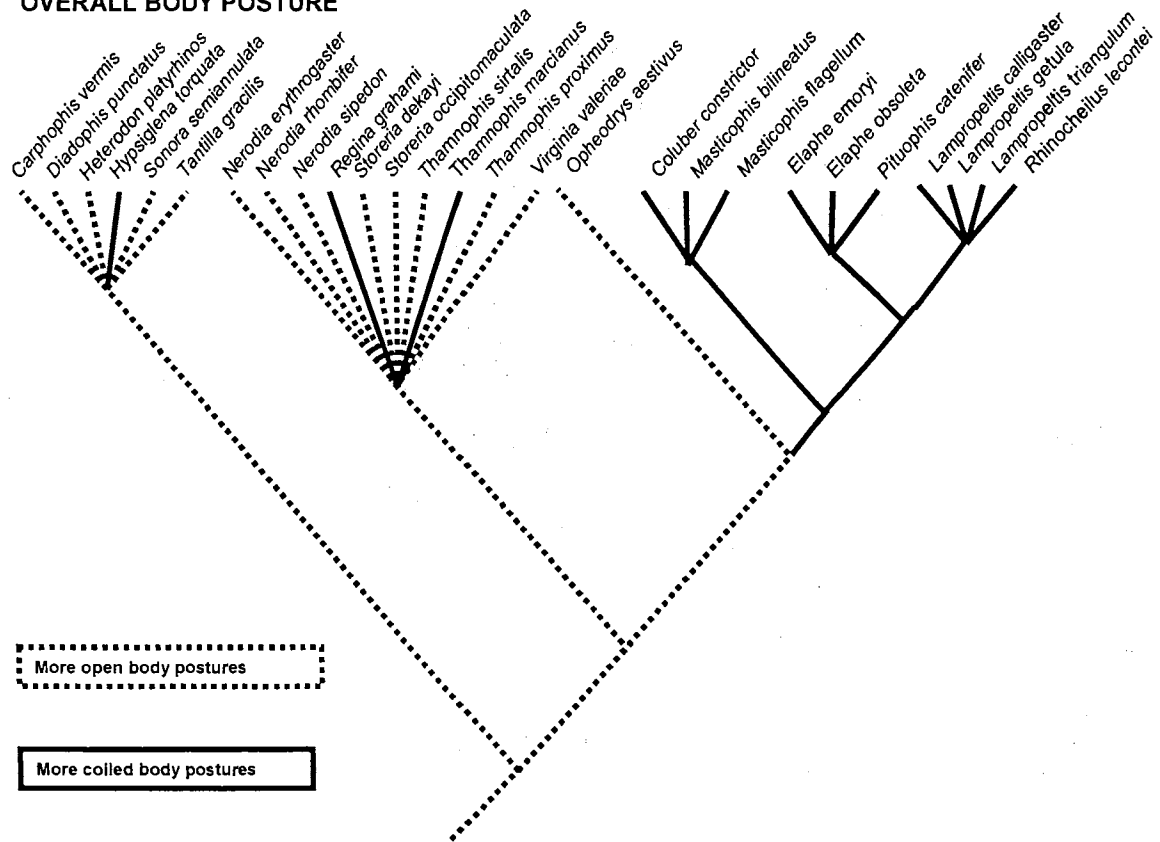


Figure 11

TAIL POSITION

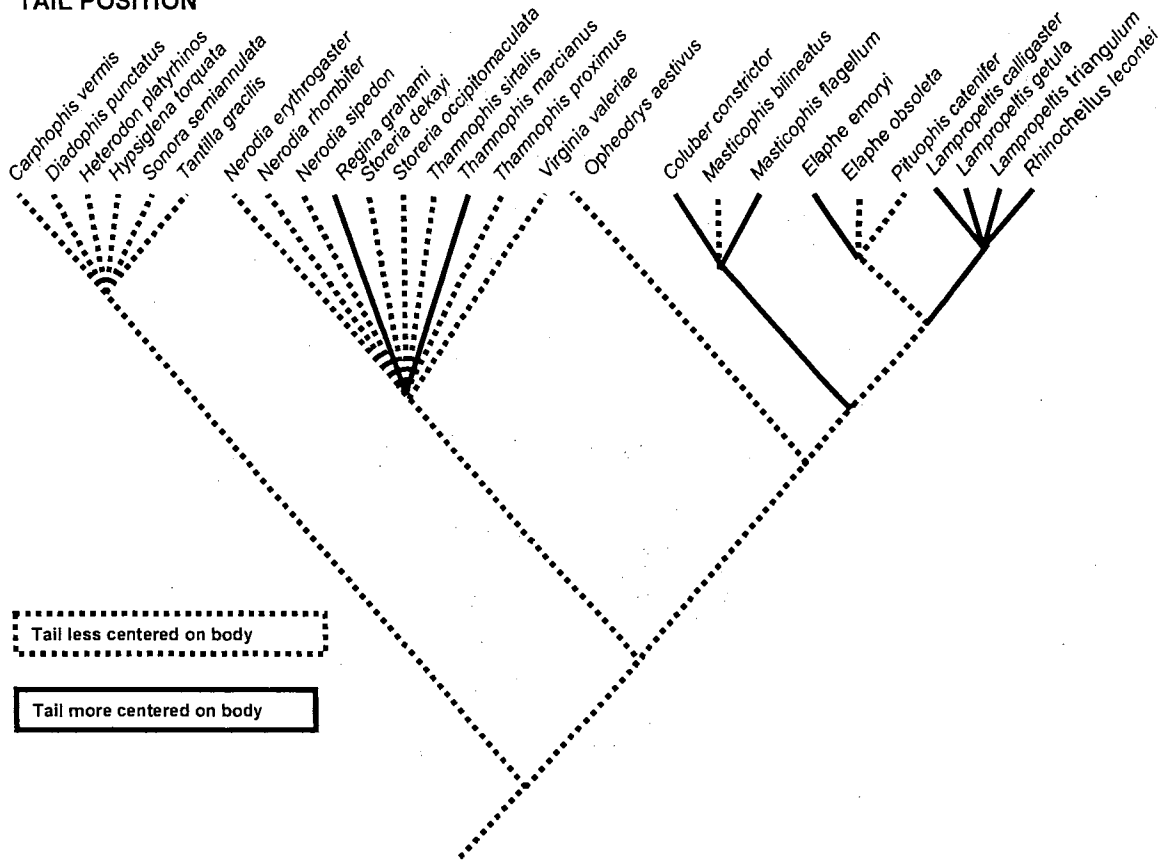


Figure 12

ESCAPE BEHAVIOR

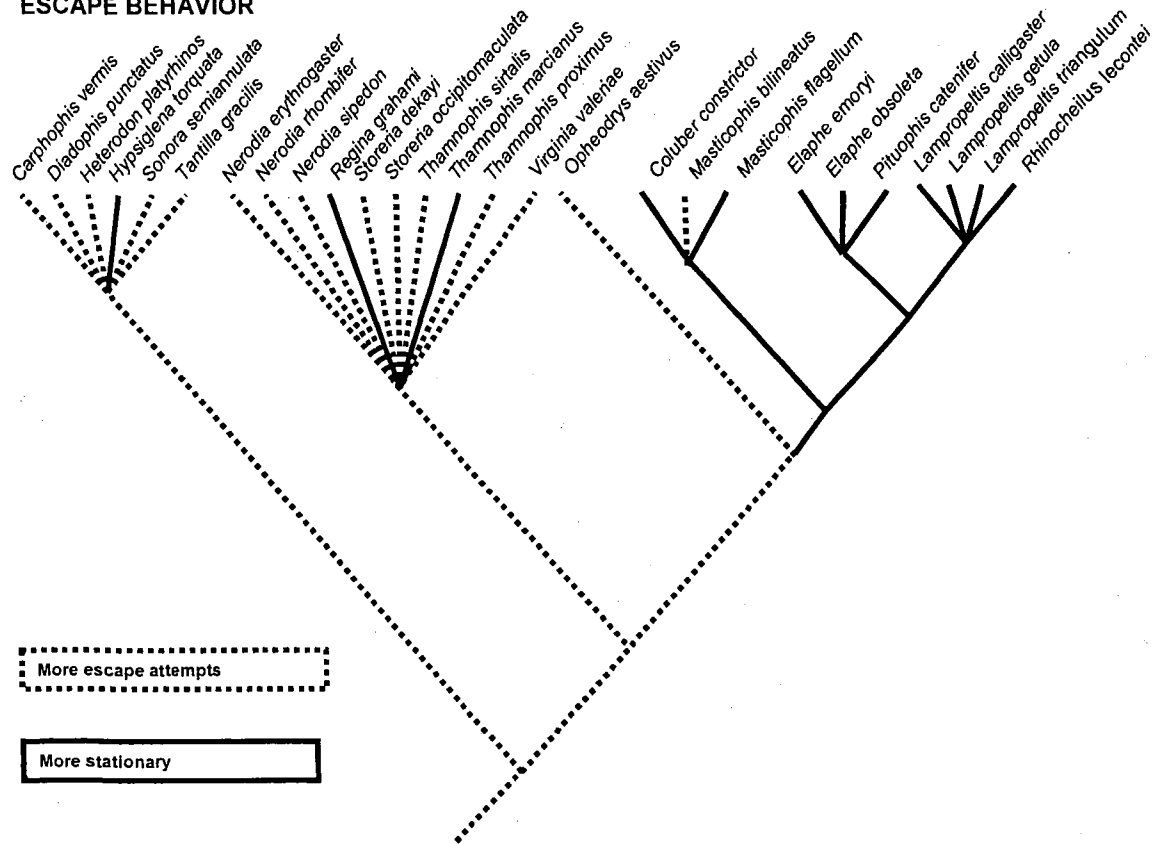


Figure 13

STRIKING BEHAVIOR

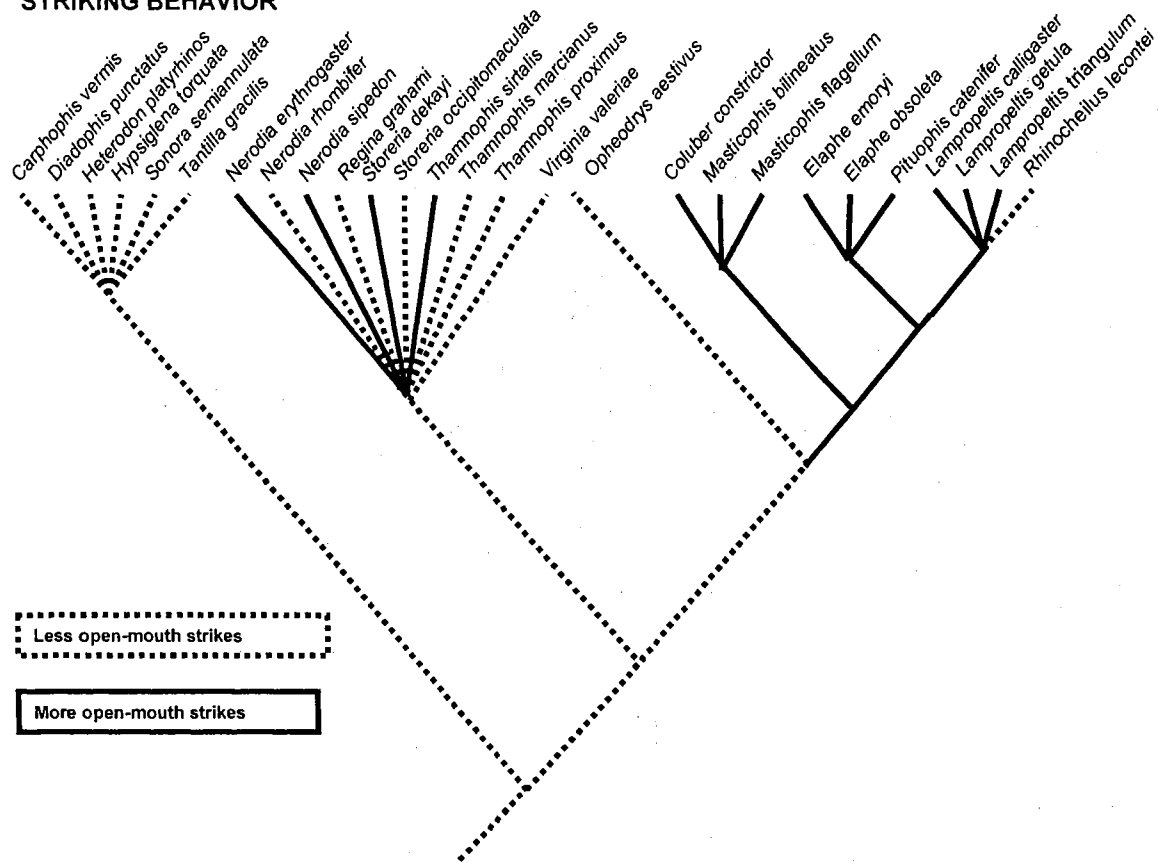


Figure 14

BODY/TAIL RUB BEHAVIOR

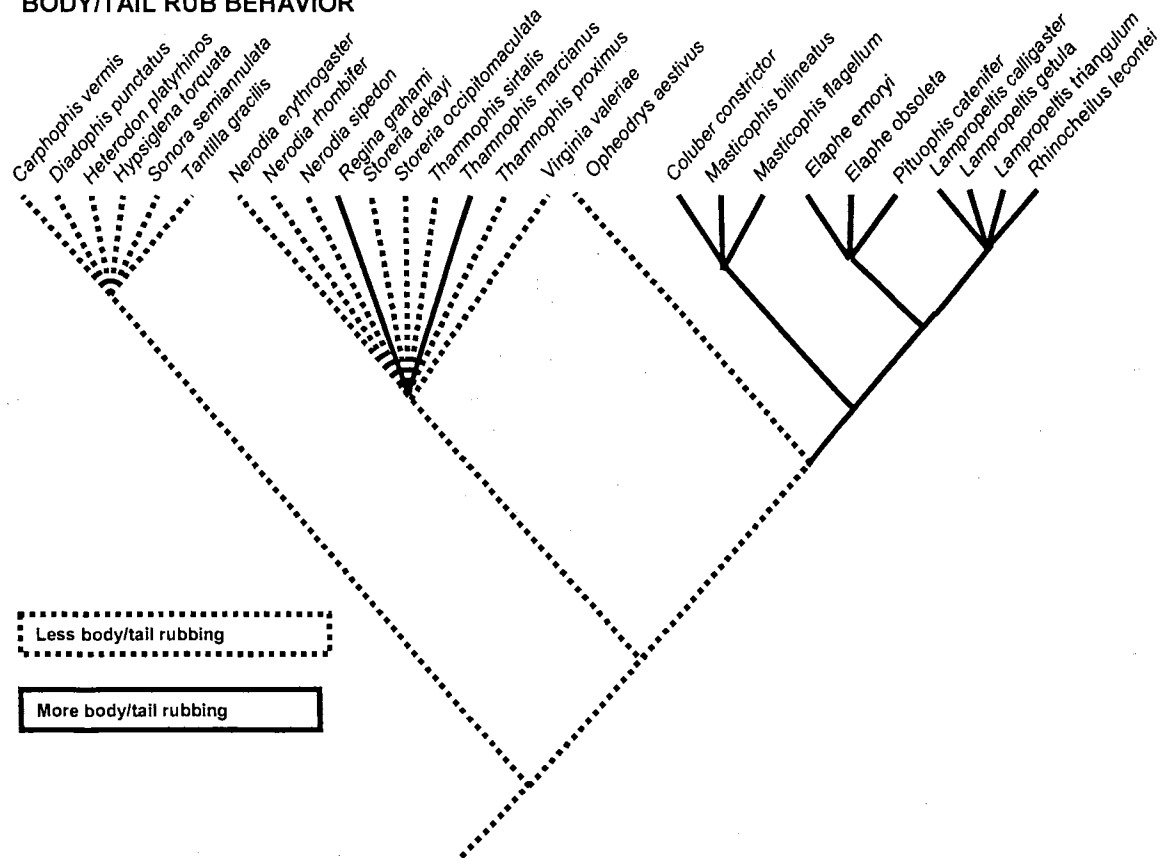


Figure 15

TAIL VIBRATION

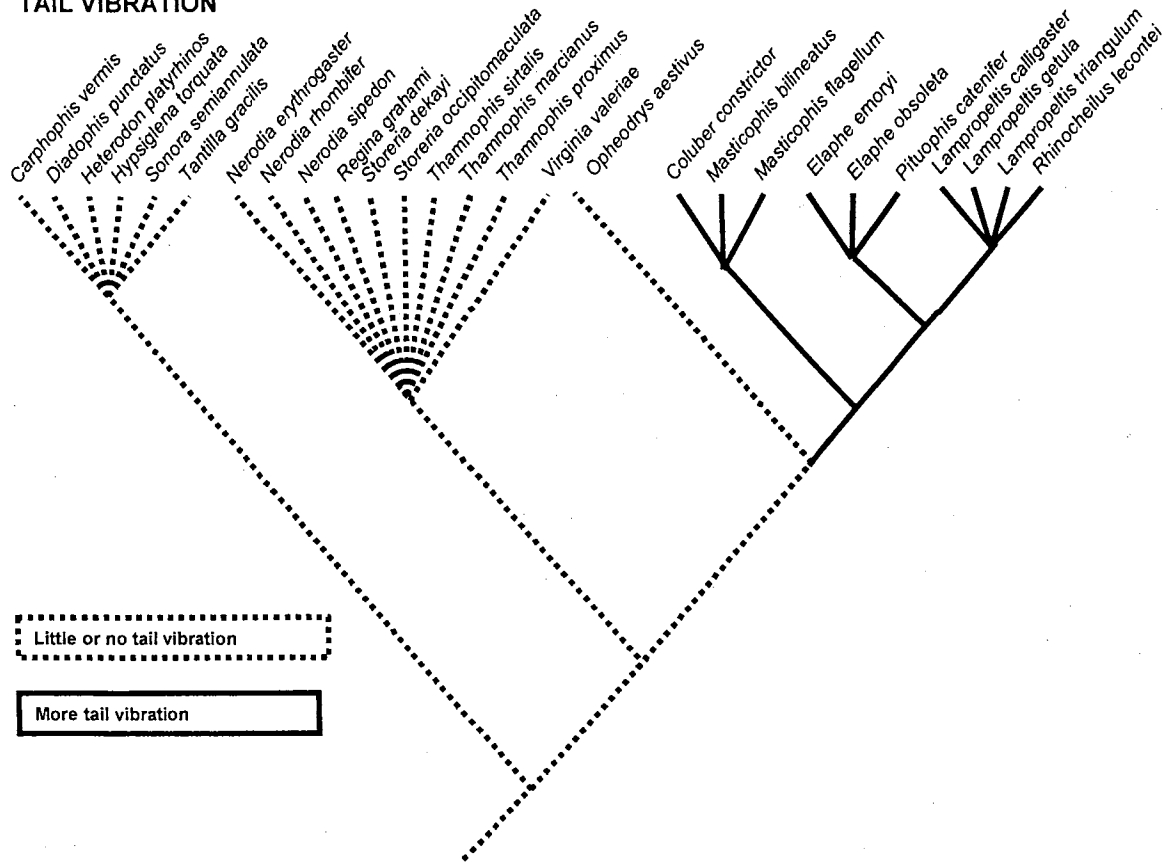


Figure 16

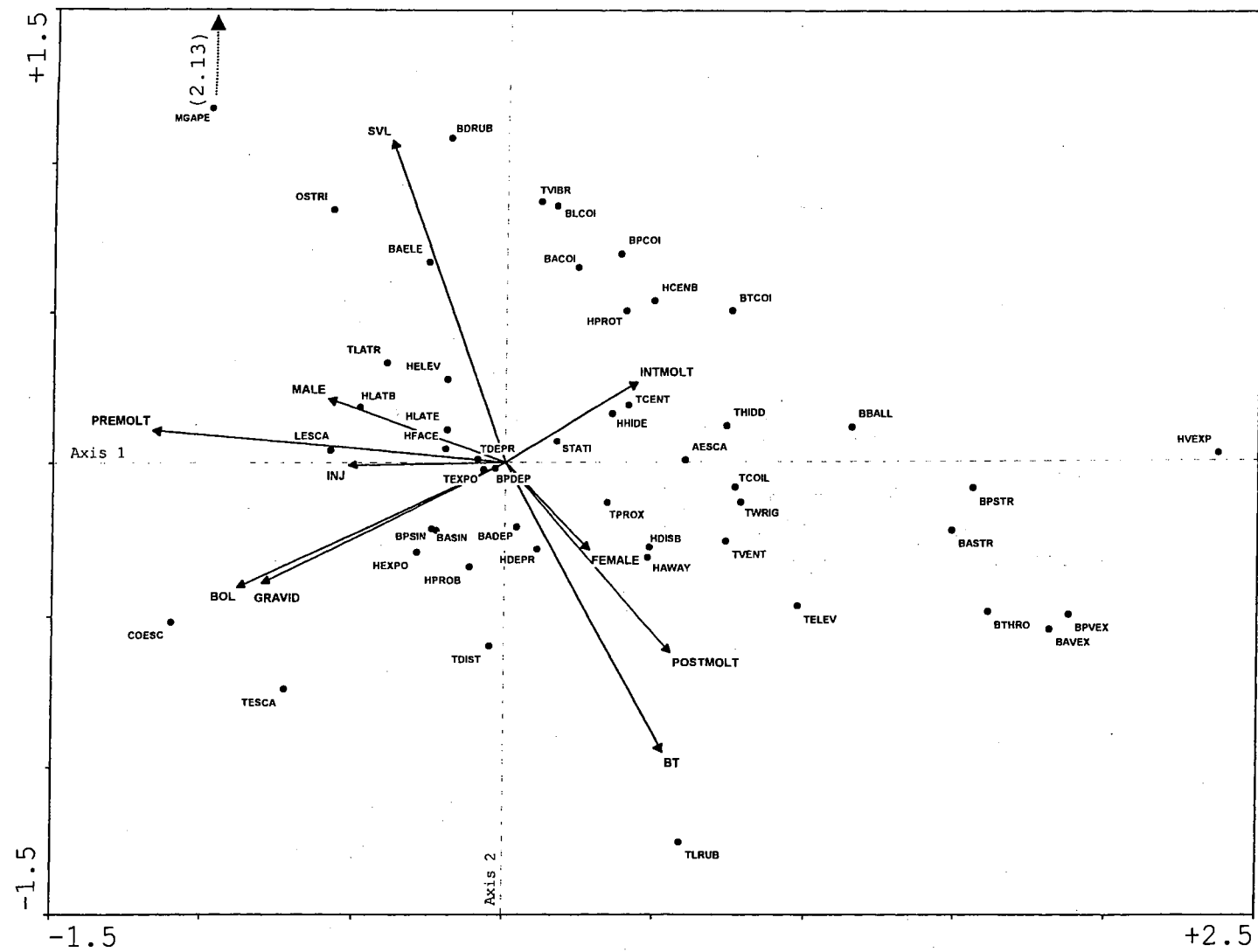


Figure 17



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Candidate for the Degree of

Doctor of Philosophy

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ULTIMATE AND PROXIMATE DETERMINANTS

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